RHODORA, Vol. 103, No. 913, pp. 1–46, 2001

SEAWEEDS OF THE BRAVE BOAT HARBOR SALT MARSH AND ADJACENT OPEN COAST OF SOUTHERN MAINE

ARTHUR C. MATHIESON

Department of Plant Biology and Jackson Estuarine Laboratory,
University of New Hampshire, Durham, NH 03824
e-mail: arthur@hopper.unh.edu

CLINTON J. DAWES

Department of Biology, University of South Florida, Tampa, FL 33620

MICHELLE L. ANDERSON

Biology Program and Jackson Estuarine Laboratory,
University of New Hampshire, Durham, NH 03824

EDWARD J. HEHRE

Department of Plant Biology and Jackson Estuarine Laboratory,
University of New Hampshire, Durham, NH 03824

ABSTRACT. A comparison of species richness at 51 coastal and estuarine sites in southern Maine is given, encompassing the area from Cape Neddick, York, to Fort Foster, Kittery, and including the Brave Boat Harbor salt marsh (York/Kittery). A total of 148 taxa was recorded, which is relatively high compared to other coastal or estuarine areas in northern New England. Seaweed populations exhibited three major distributional patterns: coastal (41%), coastal-estuarine (51%), and estuarine (8%). Perennial species dominated open coastal and outer estuarine locations, while annuals were most conspicuous at inner estuarine sites. Twenty-nine taxa were restricted to a single site (2% occurrence), whereas 19 were found at 21–36 sites (41–71% occurrence). Diversity in Brave Boat Harbor's main tidal channel was relatively high (83 species), presumably because of coastal and estuarine influences, diversity of habitats, and limited anthropogenic impacts. Six new or uncommon seaweeds were recorded from Brave Boat Harbor, including the invasive green alga *Codium fragile* subsp. *tomentosoides*, the green algal epiphyte *Urospora curvata*, the tubular opportunistic brown alga *Melanosiphon intestinalis*, the entangled or partially embedded ecads *Fucus vesiculosus* ecad *volubilis* and *F. spiralis* ecad *lutarius*, and a dwarf embedded moss or "muscoides-like" *Fucus*. The prolific growth of psammophytic populations of *F. spiralis* on sandy bluffs at Brave Boat Harbor is also unique, as it typically grows on hard substrata within contiguous muddy estuaries. It was most abundant in the outer third of the Harbor, along with its detached ecad *lutarius*. *Ascophyllum nodosum* ecad *scorpioides* and *F. vesiculosus* ecad *volubilis* grew commonly as detached or buried populations in the interior parts of the Harbor, while the "muscoides-like" *Fucus* was found on outer high sandy marsh surfaces.

Key Words: seaweeds, ecology, Brave Boat Harbor salt marsh, nearshore open coast, southern Maine.

Salt marshes in Maine are rather limited in both occurrence and areal coverage (Jacobson and Jacobson 1989; Jacobson et al. 1987). No major tidal wetlands occur within two of the state's largest embayments, Cobscook Bay in extreme eastern Washington County (an extension of the Bay of Fundy with wide-ranging tidal amplitudes and swift currents) and the sheltered Penobscot Bay region of Hancock, Waldo, and Knox Counties. Small, marginal tidal marshes occur from midcoastal Lincoln and Sagadahoc Counties to Casco Bay (Cumberland County). Further south, broad expanses of tidal wetlands in Scarborough, Wells, York, and Kittery are comparable to those of the Great Bay Estuary System of Maine and New Hampshire, the Hampton-Seabrook marsh in New Hampshire, and many large marshlands extending from the Merrimack and Parker Rivers to Cape Cod, Massachusetts.

As noted by Mann (1982), estuarine seaweeds play a variety of functional roles in northern salt marshes, including primary production, provision of critical habitat for numerous organisms, and production of abundant organic matter via detrital cycles. Although these roles are generally understood, there are few detailed assessments of seaweed communities in Maine salt marshes, except for floristic descriptions of the York River Estuary (Mathieson et al. 1993) and inner riverine sections of the Great Bay Estuary System, including the Piscataqua and Salmon Falls Rivers (Mathieson and Hehre 1986; Mathieson and Penniman 1991).

The present study is intended to characterize the species composition and variability (i.e., spatially and temporally) of estuarine and nearshore open coastal seaweed populations between Cape Neddick, York, and Fort Foster, Kittery, Maine (Figures 1–3), including those of Brave Boat Harbor (hereafter designated as BBH). The latter site represents one of three major estuaries within this area, including, from north to south (Figures 1 and 2), the York River (Maine), BBH (Maine), and the Piscataqua River (Maine and New Hampshire). The Harbor is located in the townships of York and Kittery, Maine, and is partly owned by the National Wildlife Federation/U.S. Fish and Wildlife Service with-

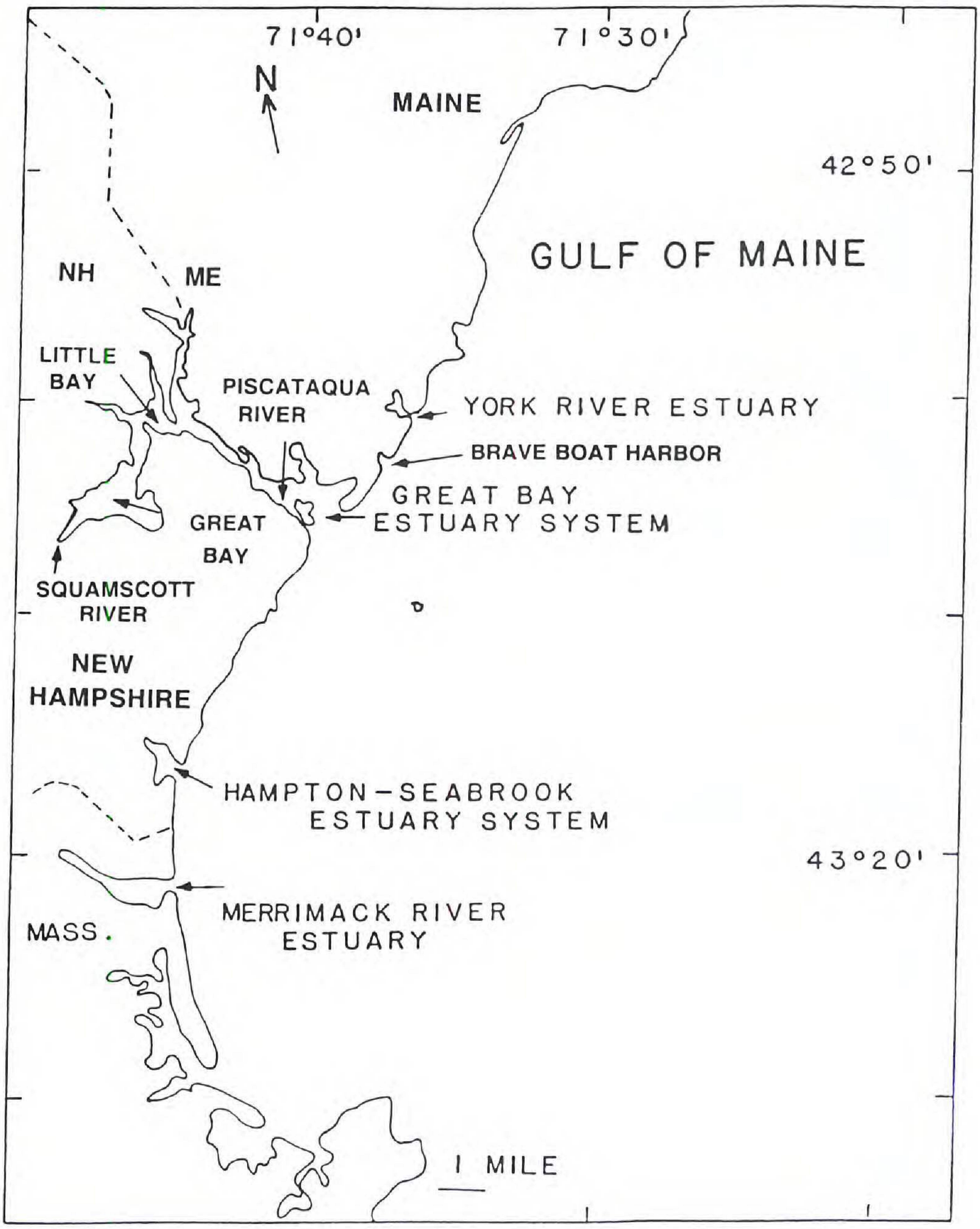

Figure 1. The coastline of northern New England between southern Maine and northern Massachusetts, showing diverse coastal and estuarine habitats.

in its Rachel Carson Wildlife Reserve (ca. 162 ha). It has a rich human history dating back to at least 1645, when sections of the marsh were alloted to residents for fodder and the rearing of cattle (archives, Kittery Historical Society). Records from the early 1700s detail the geography of BBH and its interrelationship with Gerrish Island, Cutts Island, Chauncey Creek, and the Kittery

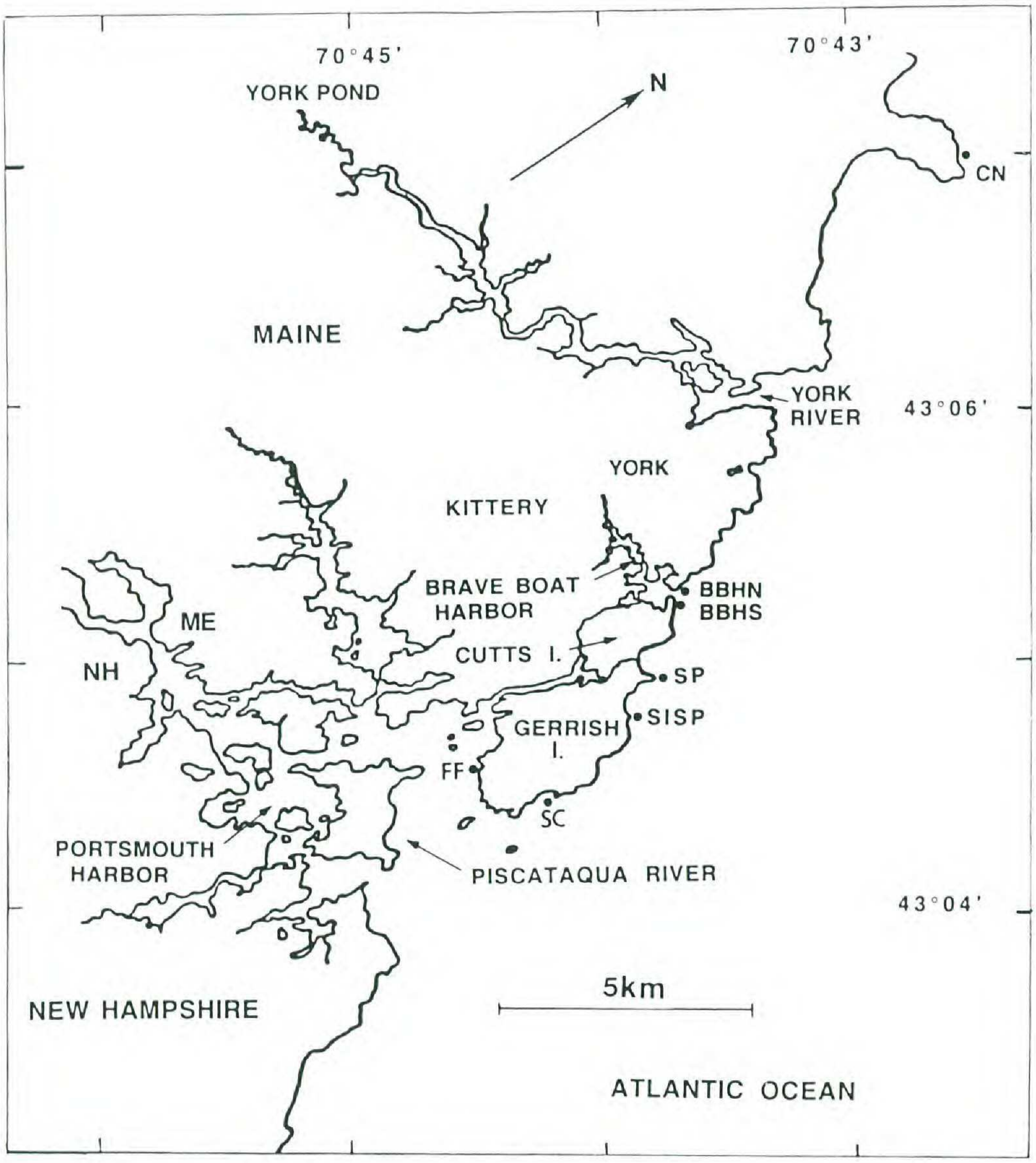

Figure 2. Southern Maine and New Hampshire coastlines, showing the location of coastal and estuarine habitats. See Appendix for abbreviations.

Point mainland (Figures 2 and 3). Both islands and Chauncey Creek are named for original settlers (cf. Samuel Drake's travel memoirs, archives, Kittery Historical Society).

The goals of our study were three-fold: (1) to compare the number and types of seaweeds from six coastal and estuarine habitats (Figures 2 and 3), including the BBH area of York/Kittery, Maine; (2) to provide a detailed floristic baseline that would aid in future conservation of these valuable habitats; (3) to compare distributional and floristic patterns in BBH with other estuaries within northern New England.

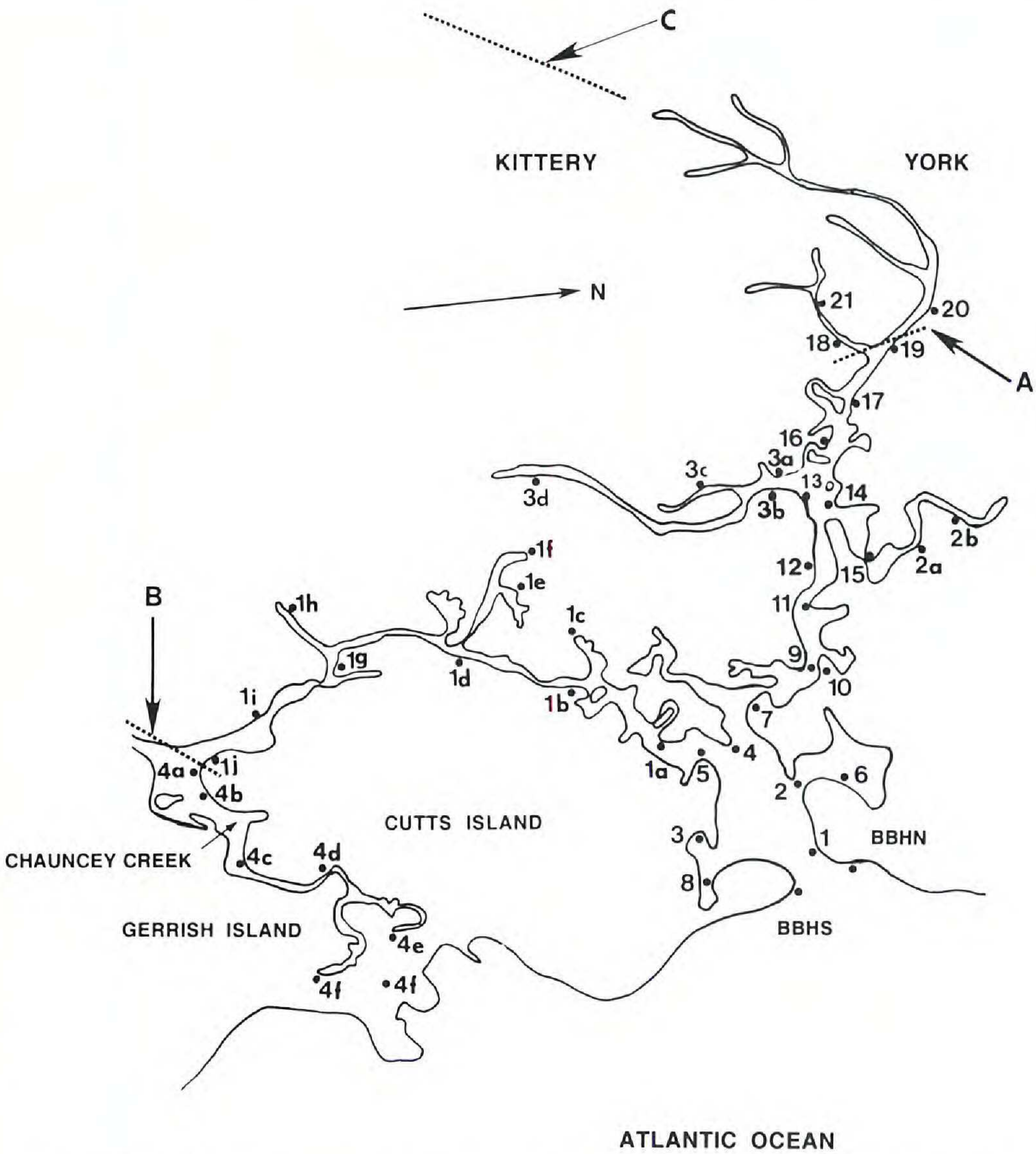

Figure 3. The twenty-one estuarine study sites along the main channel of Brave Boat Harbor (BBH), plus 23 other sites within four contiguous tidal tributaries. The dashed lines at letters "A" and "B" indicate the locations of road crossings and culvert at tributaries #1 and #4, respectively, while letter "C" designates the approximate delineation of town boundaries between York and Kittery.

MATERIALS AND METHODS

Seasonal collections were made at 51 sites in southern Maine (Figures 2 and 3; Appendix): seven nearshore open coastal locations between Cape Neddick, York (43°09.93′N, 70°35.41′W), and Fort Foster, Kittery, on the outermost Piscataqua River (43°04.0′N, 70°41.77′W); 21 estuarine sites along the main channel of BBH, York/Kittery (43°06.0′N, 70°39.33′W); 23 additional estuarine sites in four contiguous tidal tributaries of BBH and connected salt marshes (Figure 3). Descriptions of each site, including location, habitats, and substrata, are given in the Appendix. Periodic sampling of coastal populations was conducted between 1965–1985 (cf. Mathieson and Hehre 1986), while additional seasonal sampling of these and various BBH sites was done between 1997–1999.

Methods of collection and identification are similar to those of Mathieson et al. (1998), with seasonal collections of all conspicuous seaweeds from diverse intertidal (on foot) and shallow subtidal habitats (by SCUBA). Samples were returned (within one hour after being collected) to the Jackson Estuarine Laboratory, where they were identified and prepared as voucher specimens. The following taxonomic references were utilized: Adey and Adey 1973; Bird and McLachlan 1992; Blair 1983; Bliding 1963, 1968; Blomster et al. 1999; Burrows 1991; Dixon and Irvine 1977; Düwel and Wegeberg 1996; Farlow 1881; Fletcher 1987; Harper and Saunders, 2000; Hoek 1963, 1982; Irvine 1983; Irvine and Chamberlain 1994; Kingsbury 1969; Maggs and Hommersand 1993; Schneider and Searles 1991; Sears 1998; Silva et al. 1996; Taylor 1957; Villalard-Bohnsack 1995; Webber and Wilce 1971; Woelkerling 1973; Wynne and Heine 1992). The nomenclature employed primarily follows South and Tittley (1986), except for recent changes noted by Sears (1998) and Silva et al. (1996). Approximately 3500 voucher specimens documenting these studies have been deposited in the Albion R. Hodgdon Herbarium at the University of New Hampshire (NHA).

Several floristic comparisons have been made: (1) a compilation of species composition and number of taxa at each site; (2) an enumeration of percentage and mean number of total taxa for each of the six major coastal and estuarine habitats; (3) a summary of intraspecific patterns for total taxa in each habitat (e.g., the number of taxa at 21 BBH sites); (4) an assessment of number and percentage of shared taxa for each major habitat. Percent similarity values (C) were determined using Czekanowski's coefficient (Bray and Curtis 1957):

$$C = \frac{2W}{a + b}$$

where "a" is the number of taxa at the first site, "b" is the number at the second site, and "W" is the number of taxa in common to both.

Longevity characteristics were enumerated according to the scheme outlined by Knight and Parke (1931), with taxa designated as annuals (aseasonal or seasonal), perennials, or pseudoperennials, depending upon their life span, growth, and reproductive characteristics (Mathieson 1989). Delineations were based upon field studies throughout New England (Coleman and Mathieson 1975; Femino and Mathieson 1980; Hehre and Mathieson 1970; Hehre et al. 1970; Lamb and Zimmerman 1964; Mathieson 1979; Mathieson and Hehre 1982, 1983, 1986; Mathieson et al. 1993, 1996, 1998; Mathieson, Hehre and Reynolds 1981; Mathieson and Penniman 1986a, 1986b, 1991; Mathieson, Reynolds and Hehre 1981; Reynolds and Mathieson 1975; Sears and Wilce 1975; Stone et al. 1970; Webber and Wilce 1971). The number and percentage of annual and perennial taxa at each of the six major habitats were enumerated.

We compared the mean number of taxa per site in the BBH area and thirteen other estuaries between the York River in Maine and the Merrimack River in Massachusetts (Figure 1). The location, number of collecting sites, and extent of tidal limits for the BBH area are summarized in the Appendix. Similar data, based upon previous publications (Mathieson and Fralick 1972, 1973; Mathieson and Hehre 1986; Mathieson et al. 1993), is given below for the other estuarine habitats: York River, ME, 20 sites and 0–7.5 km; Piscataqua River, NH and ME, 59 sites and 0–19.4 km; Little Bay, NH, 21 sites and 13.8–19.8 km; Great Bay, NH, 16 sites and 20.6–25.1 km; Bellamy River, NH, 10 sites and 16.6–22.9 km; Cocheco River, NH, 17 sites and 20.2–25.3 km; Lamprey River, NH, 9 sites and 25.3–28.0 km; Oyster River, NH, 14 sites and 18.4–22.7 km; Salmon Falls River, NH and ME, 16 sites and 20–26.4 km; Squamscott River, NH, 16 sites and 25.9–36.3 km; Winnicut River, NH, 4 sites and 25.4–27.7 km; Hampton-Seabrook Estuary, NH, 49 sites and 0.6–5.9 km; the Merrimack River Estuary, MA, 19 sites and 0–13.7 km.

Seasonal measurements of surface water temperatures and salinities were recorded at seven sites in the main channel of BBH (Figure 3), extending from the mouth (site #1, 0.1 km inland) to tidal headwaters near Brave Boat Harbor Road (site #19, 1.6 km inland). This was accomplished using a hand-held thermometer and refractometer, with an accuracy of 0.1°C and 0.5‰, respectively. Analogous sampling was done at seven sites along tributary #1, which delineates Cutts Island and has "coastal environments" at both ends (Figure 3; Appendix). Site #1a is located 0.53 and 4.2 km from the Harbor's mouth and open coast near Sewards Cove, respectively, while #1j is 2.0 and 2.7 km from the same geographical locations. Most sampling was done at predicted low tides (Anonymous 1996), proceeding from outer to inner areas relative to the Harbor's mouth.

HABITAT DESCRIPTION AND ECOLOGY

The coastline between Cape Neddick, Maine, and Portsmouth Harbor, New Hampshire (Figure 2), has many geological and topographical features in common. These include the presence of scattered offshore islands (Boon Island and Isles of Shoals), broad arcuate bays, large rocky headlands, and scattered sandy barrier beaches in front of extensive salt marshes (cf. Mathieson and Hehre 1986). The terrain is relatively flat compared with coastal regions to the northeast. Bedrock is composed primarily of low-grade metasedimentary rock intruded by large plutons of granite and syenite (Belknap et al. 1987; Kelley 1987; Mathieson et al. 1991). Wave action on the nearshore open coast is variable, from exposed (Cape Neddick), to semi-exposed (Seapoint) and sheltered (Fort Foster). Substrata vary from massive rock outcrops to boulders, cobbles, and sand (cf. Appendix). Three major estuaries are located sequentially between Cape Neddick and Portsmouth Harbor (Figures 1 and 2): the York River Estuary, the BBH marsh complex (including the Cutts and Gerrish Island marshes), and the Piscataqua River. The York and Piscataqua Rivers are the largest estuarine habitats, extending 7.5 and 19.4 km inland, respectively; headwaters of the former are at York Pond (Mathieson et al. 1993); the latter merges into Little Bay, Great Bay, and the Squamscott River (Figure 1), extending 36.3 km inland (Mathieson and Hehre 1986). The main tidal channel at BBH is about 1.9 km in length; Cutts and Gerrish Island marshes are inner tidal tributaries and extend 0.39–4.2 and 2.4–4.2 km inland, respectively (cf. Appendix).

Brave Boat Harbor (about 2.7 km^2) is located behind a sand and cobble barrier beach near Seapoint (Figures 2 and 3; Appendix). The sand body inside the mouth of the Harbor resembles a flood tidal delta (Boothroyd 1978). However, the currents are weaker than those of classical mesotidal estuaries like the Parker River and Essex Bay in Massachusetts and provide a somewhat different configuration (Franz Anderson, pers. comm.). Tides near the mouth of BBH are uniformly semi-diurnal, with an average amplitude of about 2.6 m (Anonymous 1996). Currents and periodic inundations cause variable salinities from the mouth to the tidal headwaters at Brave Boat Harbor Road (see below).

The main channel of BBH is divided by the York and Kittery town line (Figure 3). Although it is sparsely populated and devoid of industry, shellfish harvesting is restricted to the outer Harbor due to contamination by fecal coliform bacteria. Tributaries #1 and #4 show some signs of eutrophication, presumably due to septic discharge.

The BBH salt marshes were probably formed about 10,000 years before present (YBP), following the last retreat of the Wisconsin ice sheet and subsequent stabilization of sea levels (Belknap et al. 1987; Jacobson and Jacobson 1989; Jacobson et al. 1987). Most tidal marshes in the Gulf of Maine flourished during this time, filling upper bays behind coastal sand barriers and diminishing their tidal channels into smaller creeks. Like other salt marshes between southern Maine and Massachusetts, BBH receives an abundance of fresh water (Jacobson et al. 1987). However, it is a more sandy and erosive environment than the York and Piscataqua Rivers or the Cutts and Gerrish Islands marshes (Mathieson and Hehre 1986; Mathieson et al. 1993), and it is more analogous geologically to New Hampshire's Hampton-Seabrook Estuary (Mathieson and Fralick 1972) and the Parker River area of Massachusetts (Boothroyd 1978). There is extensive erosion of BBH's outer marsh (Figure 4), possibly reflecting strong tidal currents, rising sea levels (Stevenson et al. 1986), and reduced sediments due to expansion of New England forests and increased soil conservation measures over the past 100 years. Many deep ponds and potholes occur in the outer marsh (see below), probably caused by ice rafting, surface collapse from undermining of the sand layer, and dieback of marsh grass because of wrack deposition. Thus, the outer marsh shows a patchy physiography, with extensive dissection and superficial channels.

The entrance to BBH's main channel (sites BBHN and BBHS; Figures 2 and 3) is dominated by boulders and cobbles (cf. Appendix), which were probably deposited after the retreat of the Laurentide Glacier about 50,000 YBP (Kelley 1987). Just inside

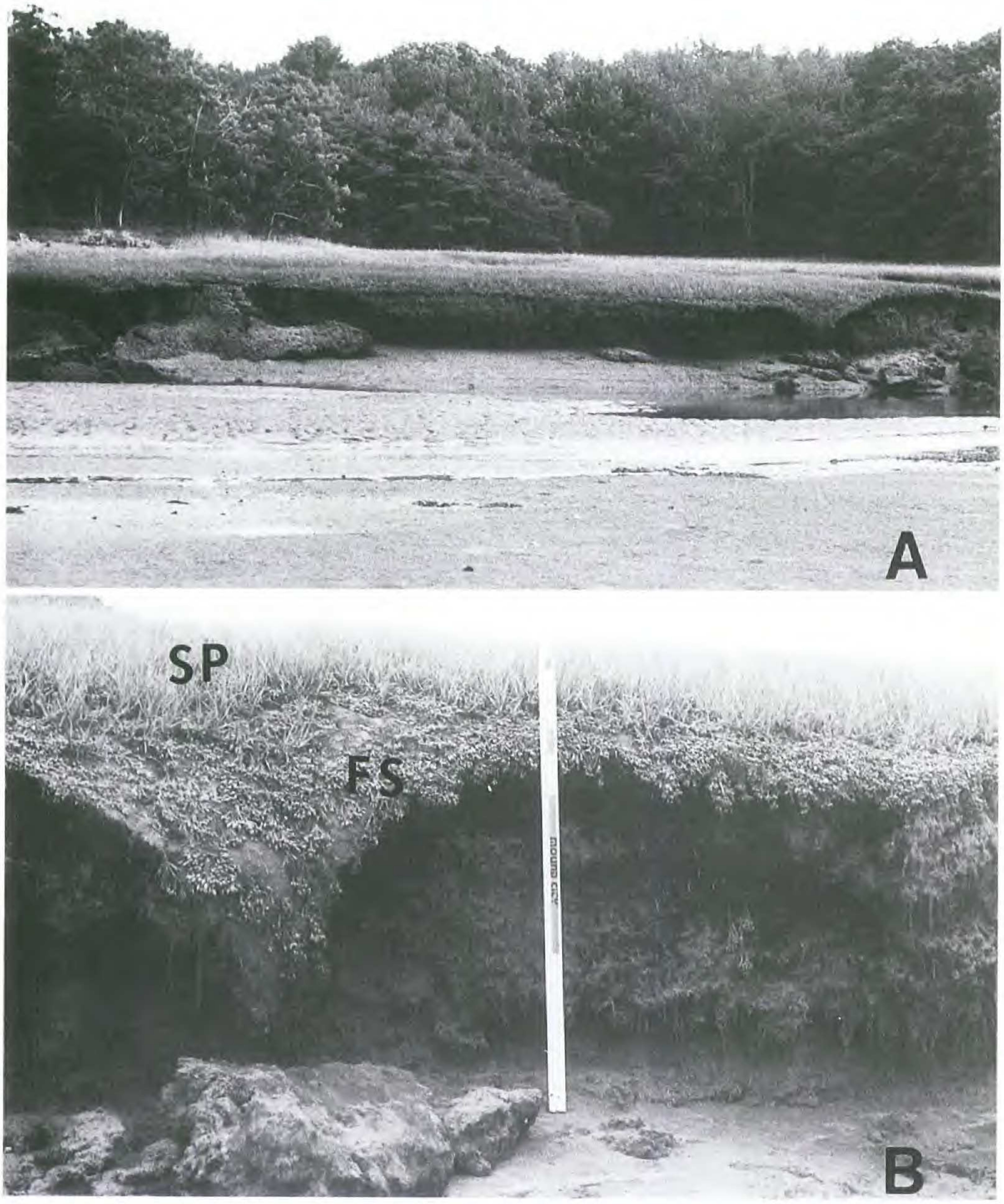

Figure 4. Photographs of the main tidal channel of Brave Boat Harbor showing (A) the broad, sandy mouth and (B) nearby eroded bluffs (1.5–3 m high) with high marsh vegetation consisting of *Spartina patens* (SP) and an understory of the dwarf muscoides-like *Fucus*. *Fucus spiralis* (FS) is attached to the sediment below the high marsh while *Pilayella littoralis* occurs as strands hanging from the cliff.

the Harbor's mouth, the shoreline is sandy and resembles a flood tidal delta (Boothroyd 1978). The exposed nature of this area is demonstrated by several features: (1) surface ripples on the sand caused by tidal currents; (2) absence of a low marsh with *Spartina alterniflora* Loisel.; (3) extensive erosion and slumping of the marsh (Figure 4A); and (4) the presence of 2 to 3 m high cliffs extending from the high marsh to bare sediment (Figure 4B). Inland, the tidal channel is sheltered, sediments are dominated by fine sand, rocky outcrops are limited, and high and low marshes occur (cf. Appendix). High marsh communities have abundant *S. patens* (Aiton) Muhl., scattered *Festuca rubra* L., *Juncus gerardii* Loisel., *Limonium nashii* Small, *Salicornia europaea* L., *Suaeda maritima* (L.) Dumort., and *Triglochin maritima* L., plus a turf-forming moss or "muscoides-like" *Fucus* (see below). *Spartina alterniflora* and the entangled/embedded understory fucoids *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus* ecad *volubilis* dominate low marshes within the middle and inner Harbor.

The first of four contiguous tidal tributaries is located on the Kittery side of the outer Harbor; it delineates Cutts Island and is exposed to "coastal" waters at both ends (Figure 3). The entrance to the first tributary (#1a) is located about 0.39 and 4.2 km inland from the open coast via the Harbor mouth and Sewards Cove, respectively (Appendix). The second tributary (#2) is located in York and extends about 1.3 to 1.7 km inland, while tributary #3 is in Kittery and extends 1.2 to 1.8 km inland. The fourth tributary, Chauncey Creek (Kittery), separates Gerrish and Cutts Islands from the mainland and from each other; it extends 2.4 to 4.2 km inland and its vegetation is similar to the inner reaches of BBH (cf. Appendix).

Water temperatures during six seasonal samplings were spatially similar throughout the Harbor, except at the two innermost sites during June and August (Figure 5A). The latter differed from open coastal sites, with temperatures of 16–18°C versus 18–23°C in June and 21–22°C versus 18–19°C in August. A strong seasonal change is evident throughout the Harbor, from 22°C in June to less than 0°C in February. Salinities near the mouth vary from 32‰ in February to 18‰ in June, the latter following a period of heavy rainfall (Figure 5B). With the exceptions of August and October, salinities decreased to 0‰ near the inner tidal dam. The stable high salinities (32‰) of August were associated with a prolonged period of hot, dry weather and limited fresh water discharge.

Figure 6 shows the effects of a "divide" in tributary #1. Salinities for February and October, 1998 were low (11–13‰) at 1.8 and 1.6 km inland from the mouth of BBH and higher (ca.

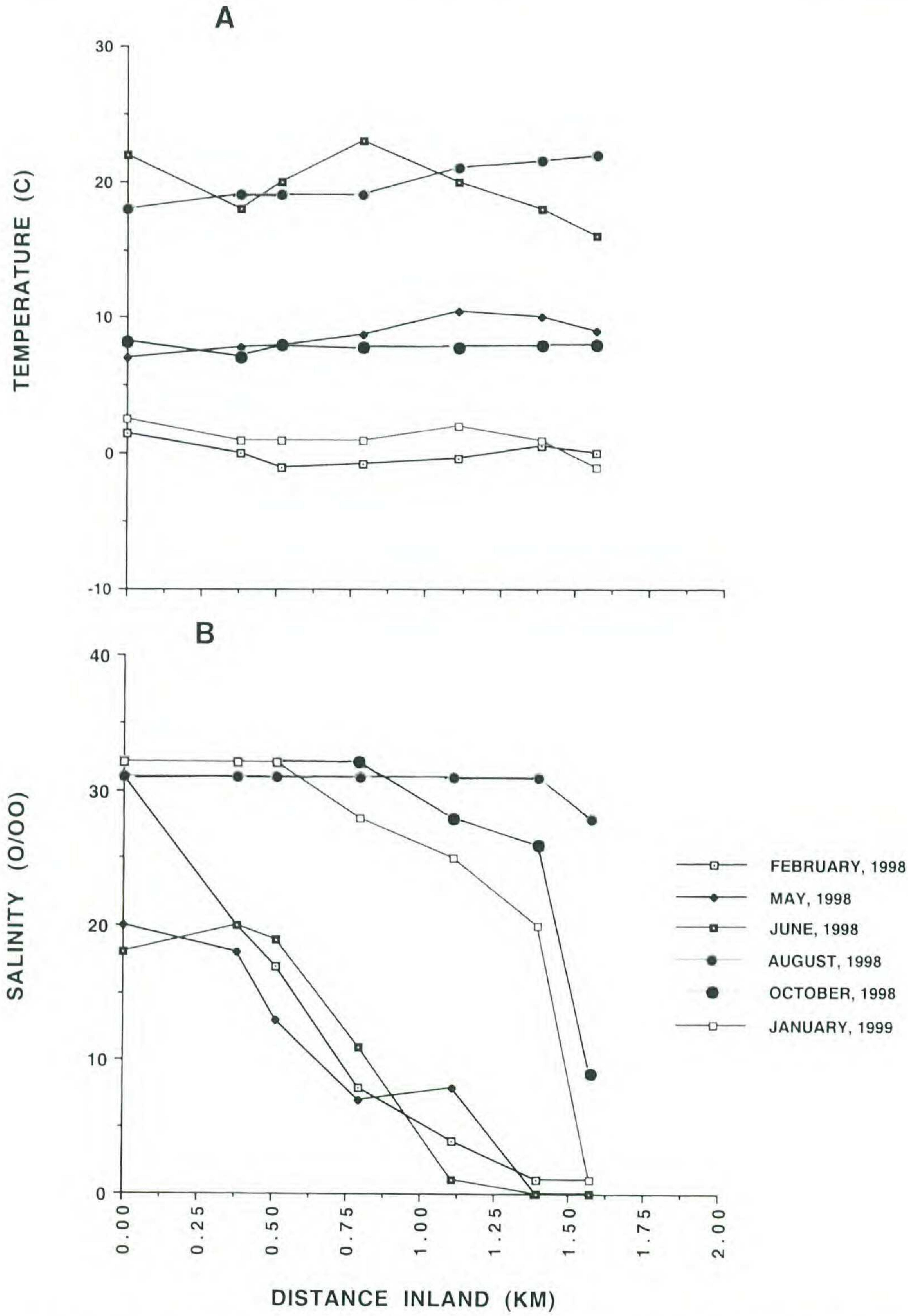

Figure 5. Surface water temperatures (A) and salinities (B) within Brave Boat Harbor during six seasonal sampling periods between February, 1998 and January, 1999. The site locations are plotted in km inland from the open mouth of the Harbor.

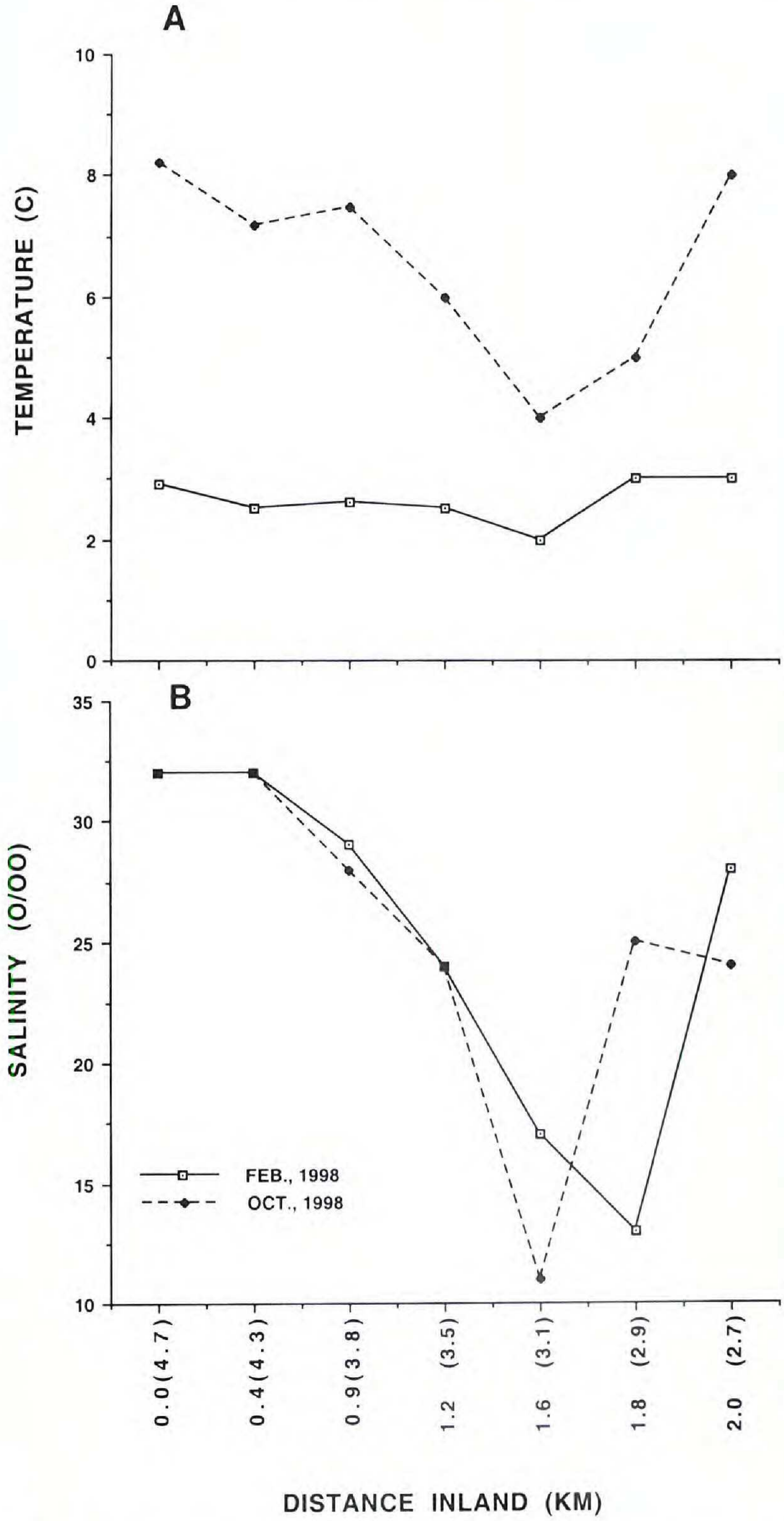

Figure 6. Surface water temperatures (A) and salinities (B) within tributary #1 that delineates Cutts Island from the main tidal channel of Brave Boat Harbor. Measurements made during February and October, 1998 show the effects of a "divide" and localized fresh water discharge. Distances (in km) represent site locations inland from the Harbor's mouth and Sewards Cove, respectively.

32‰) at both ends. Localized fresh water discharge and an enhanced elevation (a "divide") near the tributary's center cause tides to ebb in both directions. Surface water temperatures were uniform in February (2.5–3.0°C) but more spatially variable in October (4.0–8.2°C), the lowest values occurring at 1.6 km.

Ice is common during December to March within inner parts of BBH. During early winter skim ice may form on ebb tides, often disappearing on the subsequent flood tide. Over time, an "ice foot," or belt of fast-ice (Grøen 1967), freezes to the shore and does not float upwards at high tides. Typically, ice formation is greater in shallow ponds than in narrow tidal channels with stronger currents. Scouring effects are evident on rocks, pier pilings, and other substrata. Large sections of marshy shoreline may be torn loose (rafted) during spring thaws and transported to new sites (cf. Hardwick-Witman 1985, 1986; Mathieson et al. 1982).

RESULTS

Species composition and distributional patterns. A total of 148 seaweed taxa (39 Chlorophyceae, 48 Phaeophyceae, and 61 Rhodophyceae) was recorded from 51 study sites (Table 1; Figure 7). The benthic colonial diatom *Berkeleya rutilans* (Bacillariophyceae) occurred at 15 sites. Six new or uncommon taxa were recorded from BBH, including *Codium fragile* subsp. *tomentosoides, Urospora curvata, Melanosiphon intestinalis, Fucus vesiculosus* ecad *volubilis, F. spiralis* ecad *lutarius,* and the "muscoides-like" *Fucus*. The introduced siphonaceous green alga *Codium* grew abundantly in ponds near the mouth of BBH, and it was previously unknown from salt marsh habitats in Maine. The microscopic green alga *U. curvata* occurred as an epiphyte on fucoids, with its occurrence at Seapoint and BBH representing the first records of this taxon from nearshore areas in Maine. The tubular and opportunistic brown alga *M. intestinalis* was common on eroded and muddy channel embankments, while it was absent from adjacent nearshore open coastal habitats. Three detached fucoid ecads occurred as entangled or partially embedded fragments, with *Ascophyllum nodosum* ecad *scorpioides* occurring at 67% of the sites, *F. vesiculosus* ecad *volubilis* at 49%, and *F. spiralis* ecad *lutarius* at 29%. In distinguishing *F. spiralis* ecad *lutarius* and *F. vesiculosus* ecad *volubilis*, the former is a relatively narrow, proliferous, and evesiculate plant, while the latter is a broader, proliferous, and more spiraled plant that often bears vesicles (Baker and Bohling 1916; Chapman 1939). The "muscoides-like" *Fucus* (previously designated as *Fucus cottonii* M. J. Wynne *et* Magne, *F. muscoides, F. vesiculosus* variety *muscoides,* and *F. vesiculosus* ecad *muscoides*) is a minute turf-like plant that forms "lawns" in upper sandy salt marshes (Norton and Mathieson 1983). It occurred at 31% of the sites and was newly recorded from the northwest Atlantic.

Seaweed populations from the 51 study sites exhibited three major distributional patterns (Table 1; Figure 7): coastal (C), restricted to the nearshore open coast (29 red, 22 brown, and 9 green algae; 41%); coastal-estuarine (C–E), occurring in coastal and estuarine habitats (30 red, 19 brown, and 26 green algae; 51%); and estuarine (E), restricted to estuarine habitats (2 red, 7 brown, and 4 green algae; 8%).

Thirty-four of the 60 coastal taxa (57%) occurred at two or more coastal sites (including Fort Foster); the remaining 26 (43%) were restricted to a single site (Table 1). Some localized coastal taxa included *Chaetomorpha brachygona, Chorda filum, Petalonia zosterifolia, Devaleraea ramentacea,* and *Plumaria plumosa.*

Coastal-estuarine species also exhibited varying distributional patterns (Table 1). *Ascophyllum nodosum, Pilayella littoralis, Rhizoclonium riparium, Ulothrix speciosa,* and *Blidingia minima* occurred at 63–71% of the sites, while nine others, including *Hildenbrandia rubra* and *Chondrus crispus,* occurred at more than 41%. Nineteen C–E taxa were restricted to the five outermost sites and included *Bryopsis plumosa, Desmarestia aculeata, Corallina officinalis,* and *Ptilota serrata.* Twenty-seven C–E taxa had restricted (less than 20%) and patchy estuarine distributions, including *Codium fragile* subsp. *tomentosoides, Spongomorpha arcta, Dictyosiphon foeniculaceus, Laminaria saccharina,* and *Ceramium rubrum.*

Seven of the thirteen estuarine taxa (54%) were uncommon, being restricted to 1–2 sites (*Acrochaete wittrockii, Capsosiphon fulvescens, Ulothrix flacca, Punctaria tenuissima, Stictyosiphon soriferus, Polysiphonia nigra,* and *Porphyra purpurea*). By contrast, *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus* ecad *volubilis* occurred at 63% of the sites.

Frequency distribution patterns of the 148 seaweed taxa are shown in Table 1 and Figure 8. Twenty-nine taxa (4 green, 10 brown, and 15 red algae) were rare, being restricted to one site

Table 1. Summary of seaweed taxa at 51 study sites within southern Maine, including the individual site records, percent occurrence, coastal versus estuarine distributional patterns, and longevity features for each taxon; ( ) = % occurrence value, C = coastal only, C–E = coastal and estuarine, E = estuarine only, Ann. = annual, AAnn. = aseasonal annual, Per. = perennial, PPer. = pseudoperennial, " " = potential life history stage. See Appendix for habitat descriptions and abbreviations.

	Collection Sites, % Occurrence, and Longevity
BACILLARIOPHYCEAE	
Berkeleya rutilans (Trentopohl) Grünow	III, IV, VII, 3–5, 7, 9, 12, 14, 17, 1d, 1g, 1j, 3a (29%), C–E: Ann.
TOTAL DIATOM TAXA = 1	
CHLOROPHYCEAE	
Acrochaete wittrockii (Wille) R. Nielsen	7 (2%), E: Ann.
Blidingia minima (Nägeli *ex* Kützing) Kylin	I, III, IV, VI, VII, 1–5, 7–9, 12–21, 1b, 1d, 1g, 1i, 1j, 3a–3d, 4b, 4c, 4e, 4g (71%), C–E: Ann.
Bryopsis plumosa (Hudson) C. Agardh	II, 4 (4%), C–E: Ann.
Capsosiphon fulvescens (C. Agardh) Setchell *et* Gardner	1 (2%), E: Ann.
Chaetomorpha aerea (Dillwyn) Kützing	IV, VI (4%), C: Per.
Chaetomorpha brachygona Harvey	IV (2%), C: Ann. (?)
Chaetomorpha linum (O. F. Müller) Kützing	I, IV, 4, 9, 16, 1f, 1i, 1j, 4b (18%), C–E: Per.
Chaetomorpha melagonium (F. Weber *et* D. Mohr) Kützing	I, IV, VII (6%), C: Per.
Chaetomorpha picquotiana Montagne *ex* Kützing	I–IV, VII, 1, 4, 7, 9 (18%), C–E: Per.
"*Chlorochytrium inclusum* Kjellman"	IV, 1 (4%), C–E: Ann.
Cladophora albida (Nees) Kützing	I, IV (4%), C: AAnn.
Cladophora sericea (Hudson) Kützing	I, III, IV, VII, 4, 5, 7, 8, 10, 15, 16, 1j (24%), C–E: AAnn. or PPer.
"*Codiolum pusillum* (Lyngbye) Kjellman"	IV, 19 (4%), C–E: Ann.
Codium fragile (Suringar) Hariot subsp. *tomentosoides* (van Goor) P. C. Silva	I, III–V, VII, 4, 5, 7, 8 (18%), C–E: Per.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
Enteromorpha flexuosa (Wulfen *ex* Roth) J. Agardh subsp. *paradoxa* (C. Agardh) Bliding	I, IV, 9 (6%), C–E: Ann.
Enteromorpha intestinalis (L.) Ness subsp. *intestinalis*	I, IV, V, VII, 1, 3–5, 9, 12, 14, 16–19, 21, 1j, 3a–3c (39%), C–E: Ann.
Enteromorpha intestinalis (L.) Ness subsp. *compressa* Collins	IV, VII, 3, 4, 9 (10%), C–E: Ann.
Enteromorpha linza (L.) J. Agardh	I, IV, 1j (6%), C–E: Ann.
Enteromorpha muscoides (Clemente *et* Rubio) Cremades	I, IV, 3, 4, 8, 9, 14, 16, 18, 1a–1c, 1e, 2b, 3a–3c, 4a (35%), C–E: Ann.
Enteromorpha prolifera (O. F. Müller) J. Agardh	I, IV, 9, 16, 4c (10%), C–E: Ann.
Microspora pachyderma (Wille) Lagerheim	IV, 1, 2, 4, 5, 7–10, 14, 15, 17–20, 1b, 2b, 3c, 3d, 4c, 4g (41%), C–E: Ann.
Monostroma grevillei (Thuret) Wittrock	I, IV–VII, 4, 5, 14, 16, 1d, 1g, 1i, 1j, 4c (27%), C–E: Ann.
Monostroma oxyspermum (Kützing) Doty	3–5, 7, 9, 10, 15, 18, 1d, 1f, 1g, 1i, 3a–3d, 4a–4d (39%), C–E: Ann.
Percursaria percursa (C. Agardh) Rosenvinge	1–5, 7, 8 (14%), E: Ann.
Prasiola stipitata Suhr *ex* Jessen	I (2%), C: Ann.
Pringsheimiella scutata (Reinke) Höhnel *ex* Marchewianka	IV, 1, 5 (6%), C–E: Ann.
Protomonostroma undulatum (Wittrock) K. L. Vinogradova f. *pulchrum* (Farlow) M. J. Wynne	I, III, IV (6%), C: Ann.
Pseudendoclonium submarinum Wille	IV, 1, 6, 8, 9, 3c (12%), C–E: AAnn.
Rhizoclonium riparium (Roth) Harvey	I, IV, 1–5, 8–10, 12, 14–18, 1a–1c, 1e–1g, 1i, 2j, 2a, 3a–3d, 4a–4d (65%), C–E: Ann.
Rhizoclonium tortuosum (Dillwyn) Kützing	I, III, IV, VII, 1, 4, 9 (14%), C–E: AAnn.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
Spongomorpha arcta (Dillwyn) Kützing	I, IV, VII, 4, 5, 16 (12%), C–E: Ann.
Spongomorpha spinescens Kützing	I, IV, VII (6%), C: Ann.
Ulothrix flacca (Dillwyn) Thuret *in* Le Jolis	2, 20 (4%), E: Ann.
Ulothrix speciosa (Carmichael *ex* Harvey *in* Hooker) Kützing	IV, V, VII, 2–5, 7–9, 12–21, 1b, 1d, 1f–1j, 3b–3d, 4b–4e, 4g (69%), C–E: Ann.
Ulva lactuca L.	I, III, IV, VII, 1, 3, 4, 8, 9, 14, 19, 1d, 1j, 4b, 4c, 4e, 4g (33%), C–E: AAnn. or PPer.
Ulvaria obscura (Kützing) Gayral	I, IV, 14 (6%), C–E: Ann.
Urospora curvata (Printz) Kornmann *et* Sahling	IV, 4, 16 (6%), C–E: Ann.
Urospora penicilliformis (Roth) Areschoug	I, IV–VII, 1, 19, 4c (16%), C–E: Ann.
Urospora wormskjoldii (Mertens *in* Hornemann) Rosenvinge	I (2%), C: Ann.
TOTAL GREEN ALGAL TAXA = 39	
PHAEOPHYCEAE	
Agarum clathratum Dumortier	I, II, IV–VII (12%), C: Per.
Alaria esculenta (L.) Greville	I, IV, VII (6%), C: Per.
Ascocyclus distromaticus W. R. Taylor	I (2%), C: Ann.
Ascophyllum nodosum (L.) Le Jolis	I–VII, 1, 3–5, 7–9, 11, 13, 14, 16, 17, 1a, 1c, 1d, 1f, 1g, 1i, 1j, 2b, 3d, 4a–4d (63%), C–E: Per.
Ascophyllum nodosum (L.) Le Jolis ecad *scorpioides* (Hornemann) Reinke	1–18, 1a–1d, 1f, 1g, 1i, 1j, 2a, 3a–3d, 4b–4d (67%), E: Per.
Chorda filum (L.) Stackhouse	I (2%), C: Ann.
Chorda tomentosa Lyngbye	I (2%), C: Ann.
Chordaria flagelliformis (O. F. Müller) C. Agardh	I, IV (4%), C: Ann.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
Desmarestia aculeata (L.) J. V. Lamouroux	I–VII, 4, 5 (18%), C–E: Per.
Desmarestia viridis (O. F. Müller) J. V. Lamouroux	I, IV, V, 5 (8%), C–E: Ann.
Dictyosiphon foeniculaceus (Hudson) Greville	I, IV, 9 (6%), C–E: Ann.
Ectocarpus fasciculatus Harvey	IV, 5, 17 (6%), C–E: Ann.
Ectocarpus siliculosus (Dillwyn) Lyngbye	I, IV, VI, 1, 4, 5, 7, 16 (16%), C–E: Ann.
Elachista fucicola (Velley) Areschoug	I, IV, V, VII, 2–5, 8, 9, 1j, 3d (24%), C–E: Per.
Eudesme virescens (Carmichael *ex* Berkeley) J. Agardh	I, IV, (4%), C: Ann.
Fucus distichus L. *emend* Powell subsp. *distichus*	I, III, IV (6%), C: Per.
Fucus distichus L. *emend* Powell subsp. *edentatus* (de la Pylaie) Powell	I, IV (4%), C: Per.
Fucus distichus L. *emend* Powell subsp. *evanescens* (C. Agardh) Powell	I, III–VII, 1 (14%), C–E: Per.
Fucus "muscoides-like" form	2–12, 14, 17, 1b, 3a, 3c (31%), E: Per.
Fucus spiralis L.	I–VI, 1–12, 14, 16, 17, 1b, 1d, 1f, 1g, 3d (51%), C–E: Per.
Fucus spiralis L. ecad *lutarius* (Kützing) Sauvageau	2–10, 12, 14, 1i, 1j, 3a, 4b (29%), E: Per.
Fucus vesiculosus L.	I–VII, 2–4, 8, 9, 13, 15, 1d, 1f, 1g, 1i, 1j, 3c, 3d, 4a–4d (49%), C–E: Per.
Fucus vesiculosus L. ecad *volubilis* (Hudson) Turner	1–5, 7–17, 1a–1d, 1g, 1i, 1j, 2a, 3a–3d, 4b–4d, 4g (63%), E: Per.
Laminaria digitata (Hudson) J. V. Lamouroux	I, II, IV, V, VII (10%), C: Per.
Laminaria saccharina (Hudson) J. V. Lamouroux	I–VII, 4, 1j (18%), C–E: Per.
Laminariocolax tomentosoides (Farlow) Kylin	I (2%), C: Ann. (?)
Leathesia difformis (L.) Areschoug	I (2%), C: Ann.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
Melanosiphon intestinalis (D. A. Saunders) M. J. Wynne	1–5, 7, 8, 10, 14, 17, 1g, 3a, 3c (25%), E: Ann.
Mikrosyphar porphyrae Kuckuck	I, IV (4%), C: Ann.
Myrionema corunnae Sauvageau	I, IV, 1j (6%), C–E: Ann.
Petalonia fascia (O. F. Müller) Kuntze	I–VII, 1–5, 7–9, 13, 14, 16, 17, 1d, 1g, 1i, 1j, 3c, 4b–4d (53%), C–E: Ann.
Petalonia zosterifolia (Reinke) Kuntze	IV (2%), C: Ann.
Petroderma maculiforme (Wollny) Kuckuck	IV, 19, 1g (6%), C–E: Per.
Pilayella littoralis (L.) Kjellman	I, II, IV, V, VII, 1, 3–5, 9, 10, 12–19, 1b, 1d–1g, 1i, 1j, 3a–3d, 4b, 4d, 4e (65%), C–E: Ann.
Protectocarpus speciosus (Børgesen) Kuckuck	IV (2%), C: Ann.
Pseudolithoderma extensum (Crouan frat.) S. Lund	IV, 14 (4%), C–E: Per.
Punctaria plantaginea (Roth) Greville var. *plantaginea*	I (2%), C: Ann.
Punctaria tenuissima (C. Agardh) Greville	5 (2%), E: Ann.
"*Ralfsia clavata* (Harvey *in* Hooker) Crouan frat."	II–VI, 1, 4–6, 8, 14, 16, 17, 1a, 1b, 1i, 4b, 4d (33%), C–E: Per.
Ralfsia verrucosa (Areschoug) J. Agardh	I, III, IV, VI, VII, 1, 3–8, 13, 14, 16, 17, 19, 1c, 1g, 1i, 1j, 3c, 3d, 4a–4c (51%), C–E: Per.
Saccorhiza dermatodea (de La Pylaie) Areschoug	I, IV, VII (6%), C: Ann.
Scytosiphon lomentaria (Lyngbye) Link var. *lomentaria*	I–VII, 1, 3–5, 7–9, 12, 14–17, 1d, 1f, 1g, 1i, 1j, 3c, 3d, 4b, 4d (55%), C–E: Ann.
Sphacelaria arctica Harvey	I, IV (4%), C: Per.
Sphacelaria cirrosa (Roth) C. Agardh	I, III, IV, VI, VII, 3–5, 7–9, 1j (24%), C–E: Per.
Sphacelaria plumosa Lyngbye	IV (2%), C: Per.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
Sphacelaria radicans (Dillwyn) C. Agardh	IV (2%), C: Per.
Spongonema tomentosum (Hudson) Kützing	I, IV (4%), C: Per. (?)
Stictyosiphon soriferus (Reinke) Rosenvinge	5 (2%), E: Ann.
TOTAL BROWN ALGAL TAXA = 48	
RHODOPHYCEAE	
Ahnfeltia plicata (Hudson) Fries	I, III, IV, VI, VII, 1, 3–5 (18%), C–E: Per.
Antithamnionella floccosa (O. F. Müller) Whittick	I, IV (4%), C: AAnn.
Audouinella alariae (H. Jónsson) Woelkerling	I (2%), C: Ann.
Audouinella polyides (Rosenvinge) Garbary	IV (2%), C: Ann.
Audouinella purpurea (Lightfoot) Woelkerling	I, III, IV, VII (8%), C: Per.
Audouinella secundata (Lyngbye) P. S. Dixon	I, II, IV, 1, 1j (10%), C–E: Ann.
Bangia atropurpurea (Roth) C. Agardh	I, IV–VII, 5, 19 (14%), C–E: Ann.
Bonnemaisonia hamifera Hariot	I, III, IV (6%), C: Per.
Callithamnion tetragonum (Withering) S. F. Gray	IV, 1j (4%), C–E: Per.
Callocolax neglectus F. Schmitz *ex* Batters	I, IV, 5 (6%), C–E: Per.
Ceramium rubrum (Hudson) C. Agardh	I, III, IV, VI, VII, 4, 5, 7 (16%), C–E: Per.
Ceratocolax hartzii Rosenvinge	IV (2%), C: Per.
Chondrus crispus Stackhouse	I–IV, VI, VII, 2, 4, 5, 7, 8, 13, 14, 16, 17, 1d, 1g, 1i, 1j, 3c, 3d, 4d (43%), C–E: Per.
Choreocolax polysiphoniae Reinsch	I, IV (4%), C: Per.
Clathromorphum circumscriptum (Strömfelt) Foslie	I–VII, 4, 16 (18%), C–E: Per.
Coccotylus truncatus (Pallas) M. J. Wynne *et* Heine	I, III, IV, VI, VII, 4 (12%), C–E: Per.
Corallina officinalis L.	I–VII, 1 (16%), C–E: Per.
Cystoclonium purpureum (Hudson) Batters	I, III, IV, VI, VII, 4 (12%), C–E: Per.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
Devaleraea ramentacea (L.) Guiry	I (2%), C: Per.
Dumontia contorta (S. G. Gmelin) Ruprecht	I, II, IV–VII, 2, 4, 5, 7–9, 13, 14, 16, 17, 1d, 1g, 1i, 1j, 3c, 3d, 4d (45%), C–E: Ann.
Erythrotrichia carnea (Dillwyn) J. Agardh	III, IV, VI, 1, 4, 5, 8, 9, 16, 1j (20%), C–E: Ann.
Euthora cristata (L.) J. Agardh	I, III, IV, VI, VII, 1, 4, 5 (16%), C–E: Per.
Fimbrifolium dichotomum (Lepeschkin) G. I. Hansen	IV, VII (4%), C: Per.
Gloiosiphonia capillaris (Hudson) Berkeley	I (2%), C: Ann.
Gymnogongrus crenulatus (Turner) J. Agardh	I, IV (4%), C: Per.
Harveyella mirabilis (Reinsch) F. Schmitz *et* Reinke	I (2%), C: Per.
Hildenbrandia rubra (Sommerfelt) Meneghini	II, IV, VI, VII, 1, 3, 4, 6–9, 13, 14, 16, 17, 1g, 1i, 1j, 3c, 3d, 4a (41%), C–E: Per.
Lithothamnion glaciale Kjellman	I, III, IV, VII (8%), C: Per.
Lomentaria orcadensis (Harvey) Collins *ex* W. R. Taylor	I (2%), C: Per.
Mastocarpus stellatus (Stackhouse *in* Withering) Guiry	I–V, VII, 3, 4, 1g, 1j, 4b (20%), C–E: Per.
Membranoptera alata (Hudson) Stackhouse	I, IV, VI, VII (8%), C: Per.
Palmaria palmata (L.) Kuntze	I, II, IV, VII (8%), C: Per.
"*Petrocelis cruenta* J. Agardh"	I, IV, V (6%), C: Per.
Peyssonnelia rosenvingii F. Schmitz *in* Rosenvinge	II, IV, VI, VII, 6, 16, 1i, 1j (16%), C–E: Per.
Phycodrys rubens (L.) Batters	I–IV, VI, VII, 4, 5 (16%), C–E: Per.
Phyllophora pseudoceranoides (S. G. Gmelin) Newroth *et* A. R. A. Taylor	I, III–VII, 1, 3, 4 (18%), C–E: Per.
Phymatolithon laevigatum (Foslie) Foslie	I, IV, V (6%), C: Per.
Phymatolithon lamii (Me. Lemoine) Y. M. Chamberlain	IV (2%), C: Per.
Phymatolithon lenormandii (Areschoug *in* J. Agardh) W. H. Adey	II, IV, V, 1i, 1j, 4b (12%), C–E: Per.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
Plumaria plumosa (Hudson) Kuntze	I (2%), C: Per.
Pneophyllum fragile Kützing	IV (2%), C: Per.
Polyides rotundus (Hudson) Greville	I, IV, VII (6%), C: Per.
Polysiphonia flexicaulis (Harvey) Collins	I, IV, VII, 5 (8%), C–E: Per.
Polysiphonia fucoides (Hudson) Greville	I, II, IV, 2, 4, 8, 9, 1j (16%), C–E: Per.
Polysiphonia harveyi Bailey	I–VII, 1, 3–5, 7–9, 16, 17, 1j (33%), C–E: Ann.
Polysiphonia lanosa (L.) Tandy	I–VII, 4, 16 (18%), C–E: Per.
Polysiphonia nigra (Hudson) Batters	4 (2%), E: Per. (?)
Polysiphonia stricta (Dillwyn) Greville	I, IV, V (6%), C: per.
Porphyra amplissima (Kjellman) Setchell *et* Hus *in* Hus	IV (2%), C: Ann.
Porphyra leucosticta Thuret *in* Le Jolis	I, IV, VII, 4, 1j (10%), C–E: Ann.
Porphyra linearis Greville	I, IV–VII, 1, 5 (14%), C–E: Ann.
Porphyra miniata (C. Agardh) C. Agardh	I, IV (4%), C: Ann.
Porphyra purpurea (Roth) C. Agardh	4a (2%), E: Ann.
Porphyra umbilicalis (L.) Kützing	I, IV, V, VII, 1 (10%), C–E: Ann.
Porphyropsis coccinea (J. Agardh *ex* Areschoug) Rosenvinge	IV (2%), C: Ann.
Ptilota serrata Kützing	I, III, IV, VI, VII, 1, 4, 5 (16%), C–E: Per.
Rhodomela confervoides (Hudson) P. C. Silva	I, IV, V (6%), C: Per.
Scagelia pylaisaei (Montagne) M. J. Wynne	I, IV (4%), C: AAnn.
Titanoderma corallinae (Crouan frat.) Woelkerling, Y. M. Chamberlain *et* P. C. Silva	V (2%), C: Per.
Titanoderma pustulatum (J. V. Lamouroux) Woelkerling	I, IV, V, VII (8%), C: Per.
"*Trailliella intricata* Batters"	I, IV, 4 (6%), C–E: Per.
TOTAL RED ALGAL TAXA = 61	
TOTAL SEAWEED TAXA = 148	

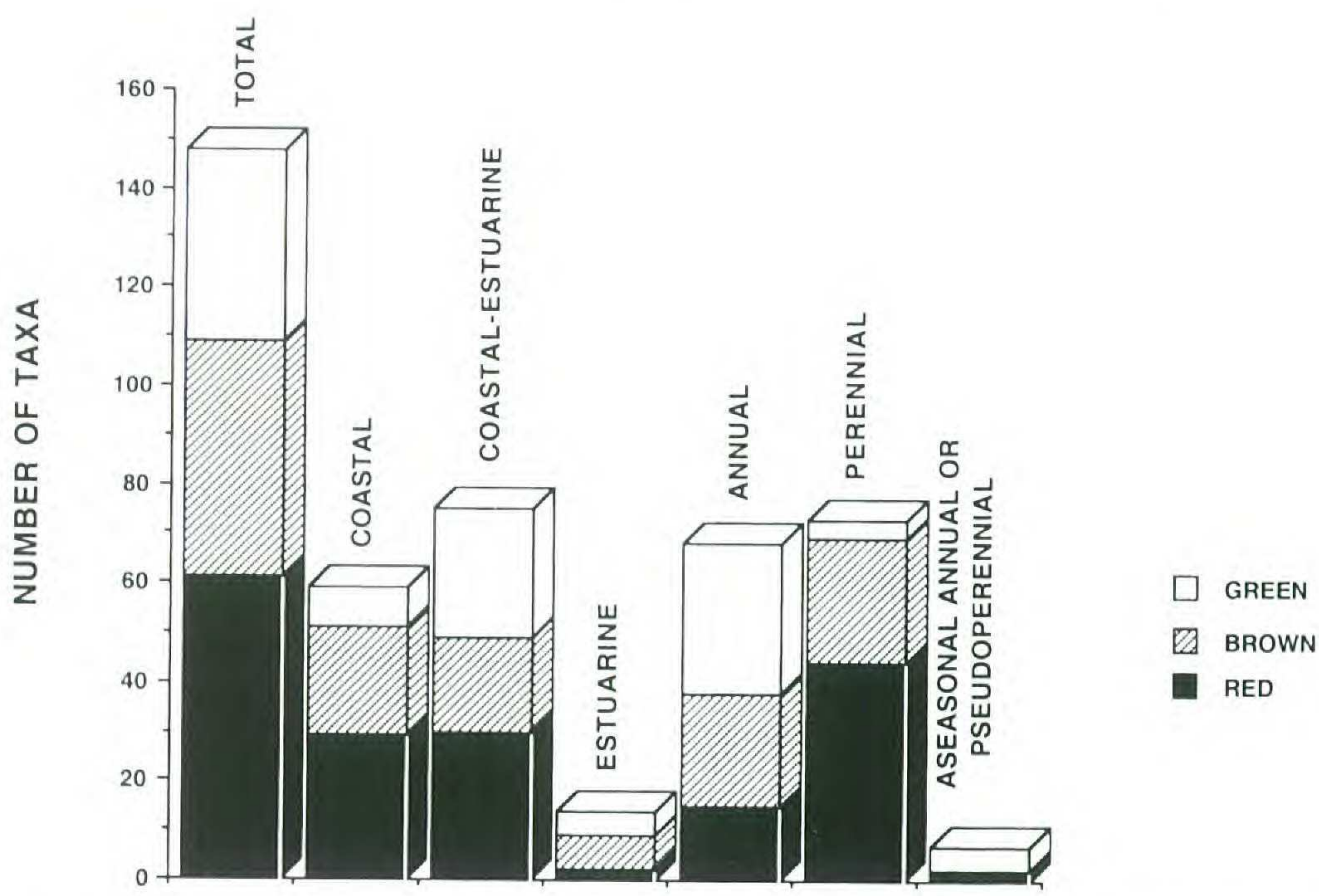

Figure 7. Patterns of species richness, local distribution, and longevity of seaweed taxa from six coastal and estuarine habitats within southern Maine.

(2.0% occurrence); 23 (7 green, 9 brown, and 7 red algae) occurred at two locations (3.9% occurrence); and 23 (8 green, 7 brown, and 8 red algae) were found at three sites (5.9% occurrence). The most ubiquitous taxa are outlined in Figure 9.

Floristic comparisons. Figure 10 illustrates patterns of species richness and floristic similarities between nearby coastal habitats, the main channel and the four tributaries of BBH (cf. Appendix). The highest total (Figure 10A) and mean number of taxa (Figure 10B) occurred on the open coast (134 taxa; 91%). The main channel had 83 taxa (56%), while the tributaries had the following number and % of total taxa: #1: 42 taxa, 28%; #4: 26 taxa, 18%; #3: 24 taxa, 16%; #2: 6 taxa, 4%. The mean number of total and shared taxa/habitat (Figure 10C) have similar patterns. The highest and most variable numbers occur on the open coast ($\bar{x}$ = 59.5 ± 35.7 and 47.3 ± 47.97 for total and shared taxa, respectively), and the lowest for tributary #2 ($\bar{x}$ = 3.0 ± 0 and 4.7 ± 1.21, for total and shared taxa, respectively). Patterns for mean percentage of shared taxa (Figure 10D) contrast with the above. The open coast and tributary #2 have the lowest percentages ($\bar{x}$ = 43.6 ± 33.8% and 33.4 ± 35.4%, respectively),

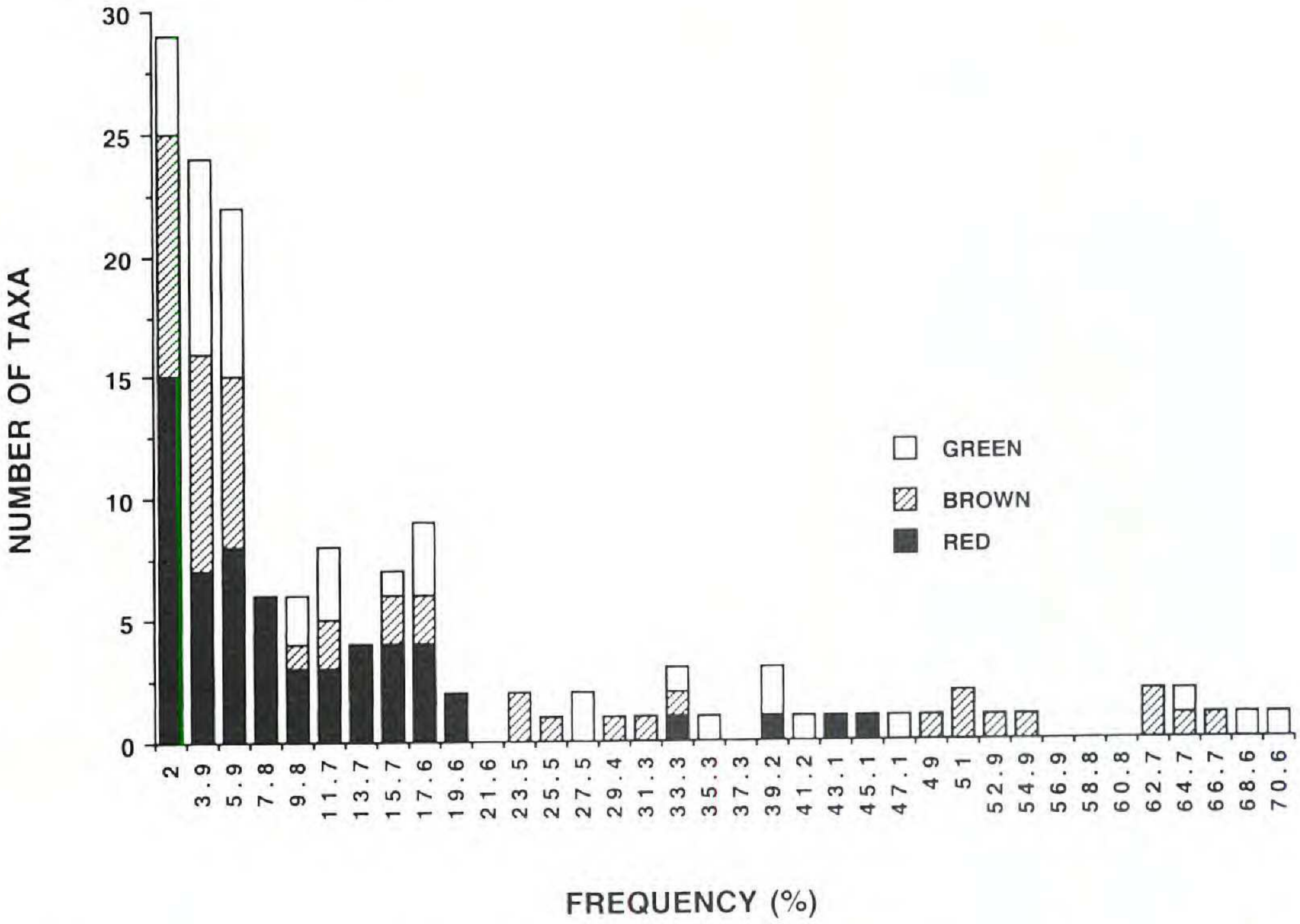

Figure 8. Frequency distribution patterns of 148 seaweed taxa recorded from fifty-one open coastal and estuarine sites in southern Maine. Taxa found at only one site (2% occurrence) are represented by the extreme left bar of the graph; those found at only two (3.9%) are represented by the next bar, etc.

while tributaries #1, #3, and #4 have the highest percentages ($\bar{x}$ = 55.6 ± 27.9% to 59.0 ± 28.7%).

Intra-habitat patterns of species richness were highly variable (Figures 11–13). Exposed open coastal areas of Nubble Light and Seapoint exhibit peak values of 102 and 117 taxa, respectively, while Sister's Point and Sewards Cove are the most depauperate with 36 taxa each (Figure 11). In the main channel of BBH (Figure 12) the highest numbers of seaweeds/site occurred just inside the mouth (sites #4 and #5), while the lowest occurred near tidal limits (site #21). Green and brown algae (particularly fucoid taxa) were widely distributed, while the reds were more circumscribed. Greens dominated inner habitats (sites #18 to #21).

Figure 13 depicts species richness in BBH's four tidal tributaries. Tributary #1 showed an enhancement of species numbers and red algae inland from the Harbor mouth. This contrasts with the pattern observed in the main channel. Site #1j is an estuarine tidal rapid with 35 taxa; it is located about 2.0 km inland from

Figure 9. Distributional frequency (%) of the sixteen most common seaweed taxa at the fifty-one study sites.

the open coast via the Harbor mouth and 2.7 km inland from Sewards Cove on Gerrish Island (cf. Appendix). Species richness and composition in #3 was lower but analogous to #1. Tributary #2 had the lowest diversity, while #4 had a similar (but reduced) pattern to that of the main channel.

Figure 14 compares the mean number (± SD) of taxa/site in BBH's main channel and four tributaries, plus 17 other estuaries. The mean number of taxa in BBH's main channel ($\bar{x}$ = 20.7 ±

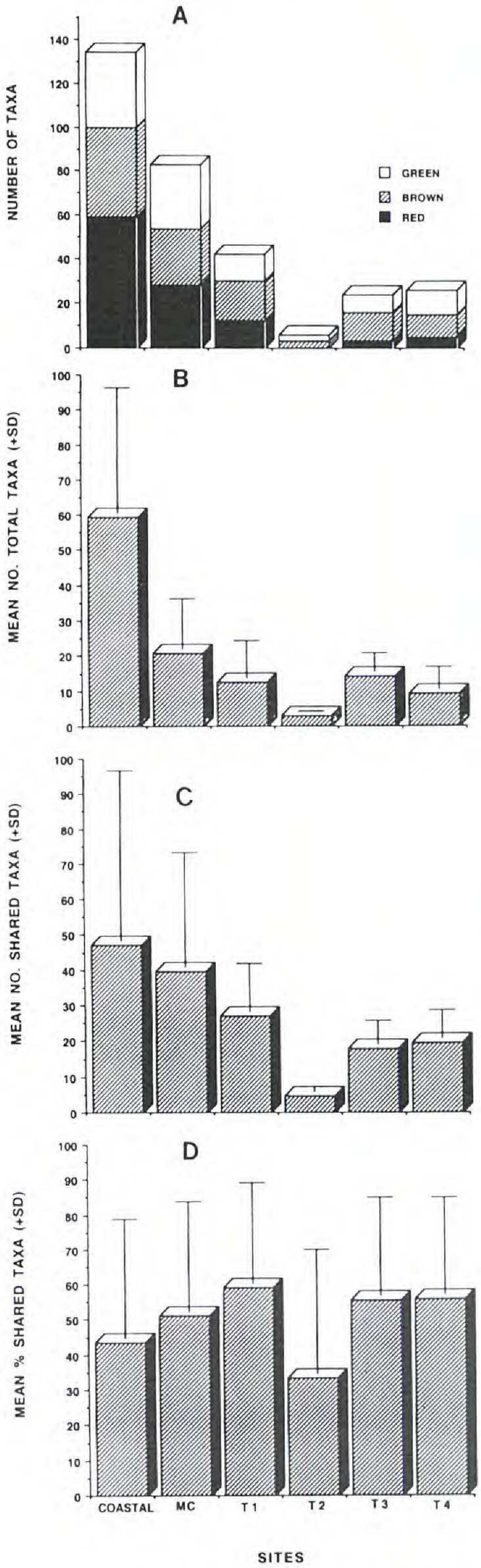

Figure 10. A comparison of the seaweed floras from six coastal sites (COASTAL), the main channel (MC), and four tributaries (#1–4) of Brave Boat Harbor. Four patterns are shown: (A) number of total red, brown, and green seaweeds; (B) mean number of total taxa; (C) mean number of shared taxa; (D) mean percentage of shared taxa. All bars are ± 1 SD. See Appendix for habitat descriptions and abbreviations.

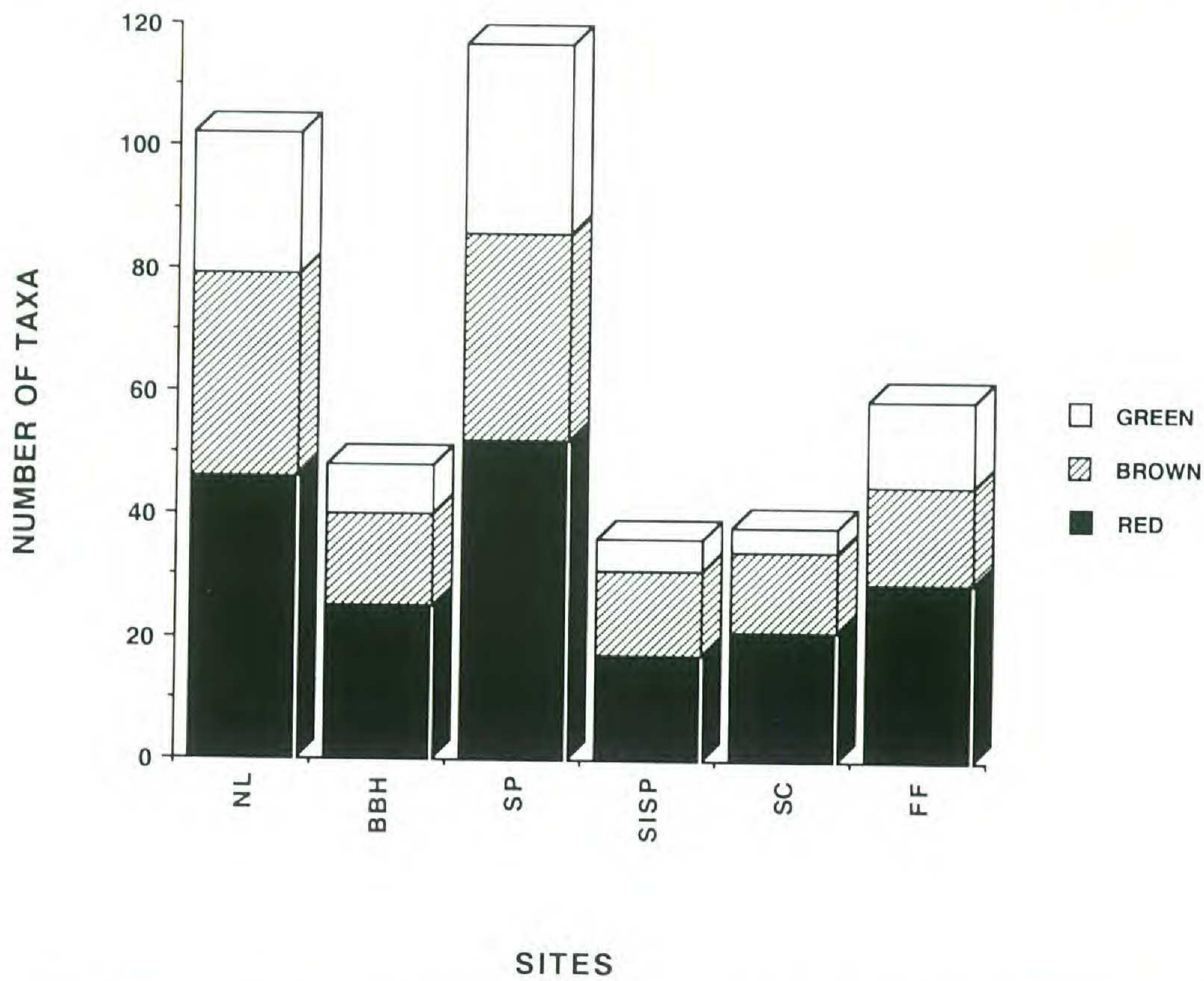

Figure 11. The number of total seaweed taxa at six nearshore open coastal sites from Cape Neddick to Fort Foster. See Appendix for habitat descriptions and abbreviations.

14.4) is less than in the Piscataqua River and Little Bay, while it is approximately the same as in the York River ($\bar{x}$ = 21.4 ± 3.2) and Great Bay proper ($\bar{x}$ = 25.3 ± 24.9). The main channel of BBH has a higher mean number of taxa than the following sites: (1) the four contiguous tributaries near BBH that vary from $\bar{x}$ = 3.0 ± 0 to 14.3 ± 5.1; (2) several mid- and inner-estuarine sites such as the Oyster River ($\bar{x}$ = 12.6 ± 7.9) and Winnicut River ($\bar{x}$ = 1.3 ± 1.6) of the Great Bay Estuary System; (3) the Hampton-Seabrook Estuary ($\bar{x}$ = 10.5 ± 5.5); (4) the Merrimack River Estuary ($\bar{x}$ = 3.5 ± 5.2). The large standard deviations recorded for the main channel of BBH, the Piscataqua River, Little Bay, and Great Bay indicate that these areas are more spatially variable than the York River and other inner estuarine habitats described above.

Longevity patterns. Sixty-eight of the 148 taxa recorded (46%) are annuals, 73 (49%) perennials, and 7 (5%) either asea-

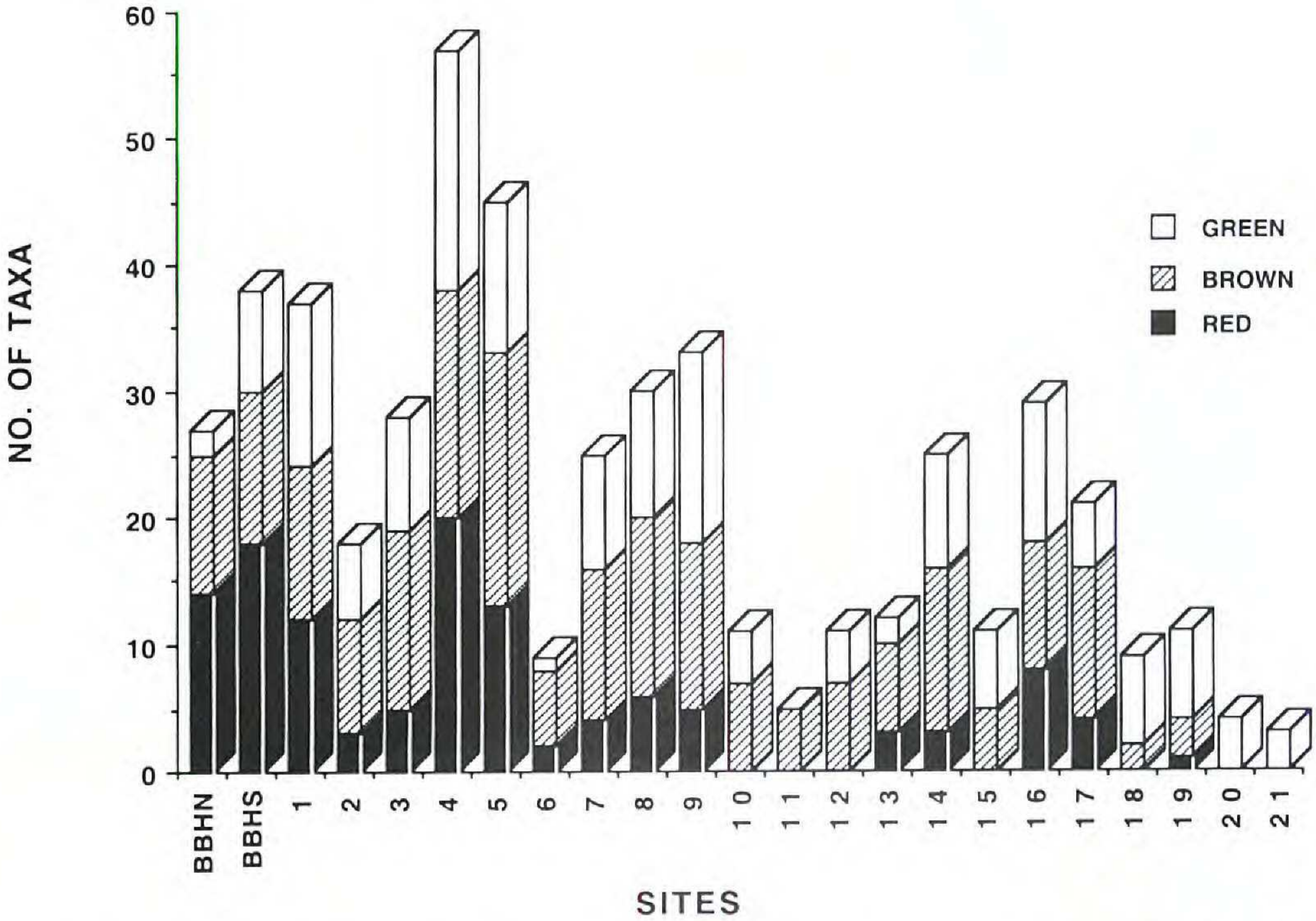

Figure 12. The number of seaweed taxa at twenty-one sites within the main tidal channel of Brave Boat Harbor and the harbor entrance (BBHN and BBHS). See Appendix for habitat descriptions.

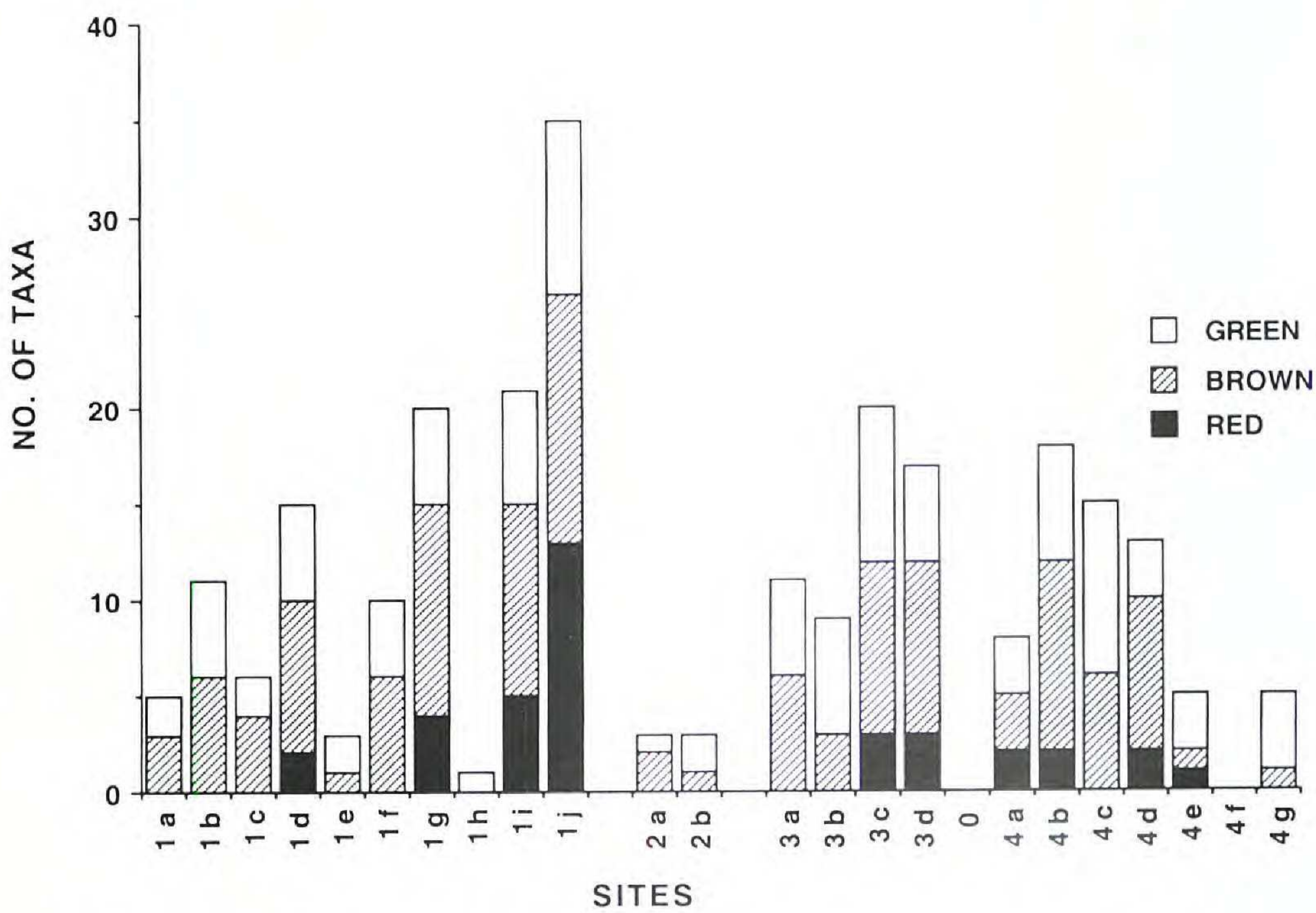

Figure 13. The number of seaweed taxa at multiple sites within four contiguous tidal tributaries (#1–4) in Brave Boat Harbor. See Appendix for habitat descriptions.

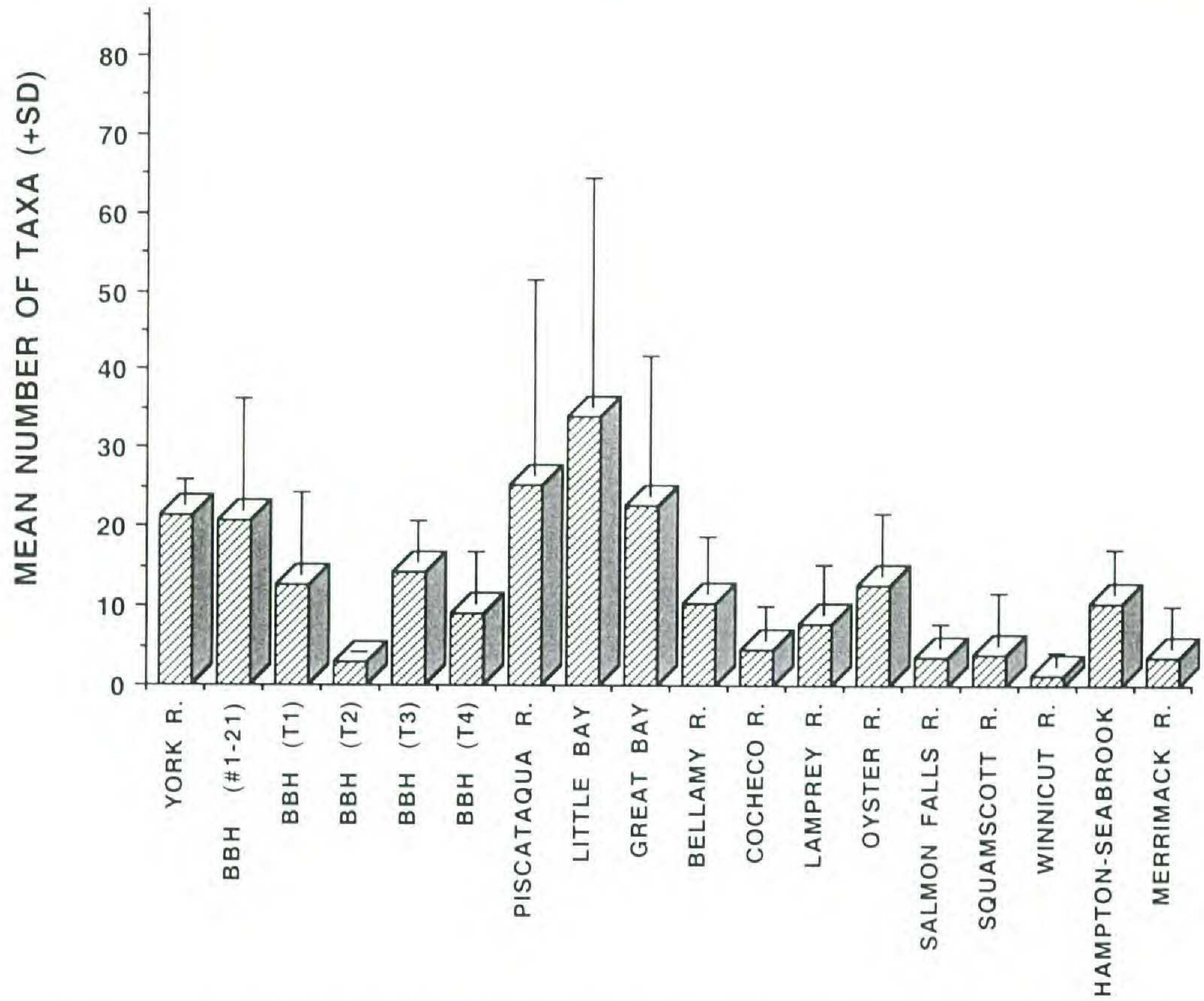

Figure 14. Mean (± SD) number of seaweed taxa/site within Brave Boat Harbor and fourteen other estuaries from southern Maine (York River) to Massachusetts (Merrimack River). See the text for a synopsis of number of collection sites/area.

sonal annuals or pseudoperennials (Table 1; Figure 7). Approximately three-quarters of the green algae (30 taxa, 77%), one-half of the browns (23 taxa, 48%), and one-quarter of the reds (15 taxa, 25%) are annuals. The ratios of annuals to perennials (Figure 15A, B) are analogous to those previously described, showing only modest differences: (1) open coast, 63/134, 47%; (2) BBH main channel, 43/83, 51.8%; (3) tributary #1, 18/42, 42.8%; (4) tributary #2, 3/6, 50%; (5) tributary #3, 14/24, 58.3%; (6) tributary #4, 13/26, 50%.

DISCUSSION

Species richness within the 51 southern Maine sites is relatively high (148 taxa) compared with other Northwest Atlantic sites. For example, 216 taxa are recorded from over 200 coastal and estuarine sites in New Hampshire and southern Maine

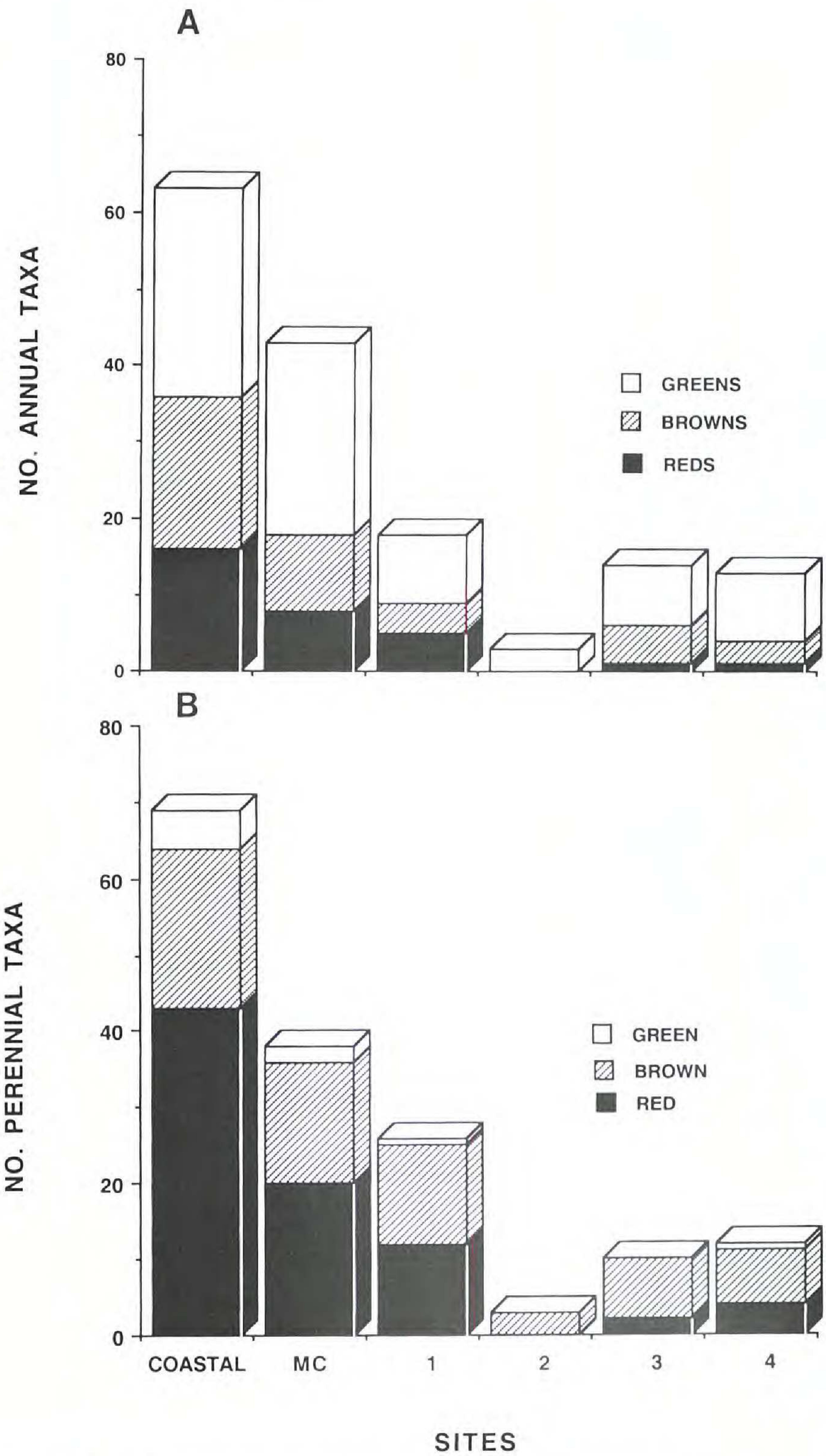

Figure 15. A comparison of the number of annual (A) and perennial (B) red, brown, and green seaweeds from six coastal sites (COASTAL), the main tidal channel (MC), and four tributaries (#1–4) of Brave Boat Harbor. See Appendix for habitat descriptions and abbreviations.

(Mathieson and Hehre 1986), which include 179 taxa from the nearshore open coast between Portsmouth and Seabrook (NH), 164 from the Isles of Shoals (ME and NH), 161 from the Great Bay Estuary System (NH and ME), and 63 from the Hampton-Seabrook Estuary System (NH). Although the numbers recorded for the Shoals and Great Bay Estuary System are similar, their species composition is quite different, presumably because of pronounced habitat variations (Mathieson and Penniman 1986b). Maine's two largest embayments (Penobscot and Casco Bays) have 139 and 194 taxa, respectively (Collins 1911; Farlow 1881; Mathieson et al. 1996). The numbers of taxa from insular habitats throughout the Gulf of Maine range from 145 on Mount Desert, the largest coastal island (Collins 1894; Mathieson et al. 1998), to 136 on Smuttynose Island, Maine, and 4–65 taxa/island in Penobscot Bay (Mathieson et al. 1996, 1998). Penikese Island, just south of Cape Cod, Massachusetts, has 131 taxa (Doty 1948; Jordan 1874; Lewis 1924). Newfoundland, the largest and most extensively studied northeastern Canadian island, has about 254 taxa (South 1983; South and Hooper 1980), while Tittley and colleagues (1987) have recorded 159 taxa from Passamaquoddy Bay, New Brunswick, Canada.

There is a conspicuous reduction in species richness within the six southern Maine habitats (Figure 10); the highest numbers of taxa and perennial seaweeds occur on the open coast. A combination of physical factors is probably responsible, including enhanced water motion, greater availability of rocky substrata, and more stable hydrographic conditions (Coutinho and Seeliger 1984; Doty and Newhouse 1954; Hartog 1971; Josselyn and West 1985; Ketchum 1983; Mathieson and Penniman 1986a, 1991; Wilkinson 1980). Brave Boat Harbor is more turbid and sedimented and has greater hydrographic variability than the nearby open coast (Figures 5 and 6). Inner estuarine areas of BBH have steep tidal channels and dissected salt marshes, which are dominated by reduced floras of ephemeral (opportunistic) green algae (Table 1). Physical extremes probably determine the distributional limits and potential for perennial longevity where physiological tolerances are approached (cf. Fralick and Mathieson 1975; Guo and Mathieson 1992; Kinne 1970, 1971; Penniman and Mathieson 1985). For example, within the inner reaches of the Great Bay Estuary (i.e., Great Bay proper) hydrographic variability is approximately two (temperature) to five times (salinity) greater than on the adjacent open coast near Portsmouth (Loder et al. 1979, 1983a,1983b; Norall et al. 1982). Similar, but more circumscribed patterns are present in the BBH area (cf. Figures 5 and 6), and seasonal extremes in temperature and salinity are evident in the Harbor's interior. Unlike the land-locked and muddy inner parts of the Great Bay Estuary, the outer third of BBH is directly connected to the open ocean and has a sandy substratum. Thus, BBH's flora consists of many oceanic species at its mouth and a few estuarine ones at its tidal limits.

A comparison of the mean number of taxa/site in BBH and the York, Piscataqua, and Merrimack Rivers, is instructive as all four estuaries are contiguous with the open coast and in close proximity (Figures 1 and 14). The York River and BBH exhibit similar patterns, the Piscataqua River is more diverse, and the Merrimack River is very depauperate. There are varying levels of eutrophication and development in the four estuaries: BBH has circumscribed fecal coliform contamination (see above); the York River has limited housing development and eutrophication; and the Piscataqua and Merrimack Rivers have intermediate to high levels of industrial development and eutrophication, respectively (cf. Mathieson and Fralick 1973; Mathieson and Penniman 1986a; Mathieson, Reynolds, and Hehre 1981; Mathieson et al. 1993). The Merrimack River is one of the most polluted in New England and is also one of the major sources of fresh water discharge into the Gulf of Maine (Anonymous 1984, 1987; Appolonio 1979; Jerome et al. 1965; Miller et al. 1971). Within the same four estuaries, the Piscataqua River has the greatest diversity of habitats, with tidal rapids, salt marshes, and stable substrata, all of which combine to support a diverse seaweed flora. In summary, the mean number of taxa/site in BBH exceeds the values for the Merrimack River, the contiguous BBH tributaries, and several mid- and inner-estuarine sites. Low species diversity is a typical response to stresses such as pollution, development, and extreme hydrographic variability where only a few tolerant ulotrichalean green algae such as *Enteromorpha, Monostroma, Ulva,* and *Ulvaria* dominate (Cotton 1910; Fritsch 1935; Sawyer 1965; Wilkinson 1980).

Intra-habitat diversity patterns are determined by the same suite of physical factors. Differential wave action, stability of substrata, and habitat variability are key factors determining spatial differences of coastal communities (Mathieson et al. 1991). The extreme variability of floras at Seapoint and the mouth of Brave Boat Harbor (BBHN and BBHS) is a case in point (Figure 11), with both sites exposed to strong wave action. Seapoint has a greater diversity of habitats and rocky outcrops and the mouth of BBH is dominated by cobbles and boulders that move in storms (cf. Appendix). The higher diversity of seaweeds in BBH's main channel compared with its tributaries may also be explained by differential availability of solid substrata and varying hydrographic conditions. The main channel has scattered boulders, rocks, and pebbles, plus the remains of an old wooden railroad trestle; the tributaries have more limited and scattered solid substrata (particularly #2). Sporadic peaks of species diversity are probably associated with enhanced substrata and water motion. For example, the highest number of species in tributary #1 occurs at the bridge culvert on Seapoint Road (#1j), where strong currents, abundant rocks, and a fringing marsh are present. By contrast, sites #1h and #1i are impounded and do not totally drain at low tide, reducing the numbers of taxa. Sporadic patterns are evident in the third and fourth tributaries, where localized populations of *Chondrus crispus, Dumontia contorta,* and *Hildenbrandia rubra* grow in narrow tidal channels with strong currents and rocky substrata (cf. Table 1; Figure 13). As noted by Lewis (1964, 1968) tidal rapids have high concentrations of dissolved gases (oxygen and carbon dioxide) and reduced sediments, which allow enhanced colonization by open coastal and perennial seaweeds (Mathieson et al. 1977, 1983; Reynolds and Mathieson 1975).

Seaweed longevity patterns in BBH reflect the above-described physical factors. Outer floras are dominated by perennial taxa, while annuals exhibit broader distributions, often dominating inner estuarine habitats. *Blidingia minima, Enteromorpha* spp., *Microspora pachyderma,* and *Rhizoclonium riparium* are conspicuous annual green algae that form extensive mats amongst marsh grasses. Perennial greens are few in number and primarily occur in the main channel or in deep outer pools (*Codium*). Perennial brown and red algae (e.g., *Ascophyllum nodosum, Laminaria saccharina, Chondrus crispus, Hildenbrandia rubra, Phymatolithon lenormandii,* and *Polysiphonia fucoides*) exhibit either analogous coastal patterns or are found in localized areas of strong tidal currents. Conspicuous annuals include *Dumontia contorta, Melanosiphon intestinalis, Petalonia fascia,* and *Scytosiphon lomentaria* var. *lomentaria.*

The fucoid algae found in BBH are of special interest because of their diversity, habitat preferences, and abundance. Prior to the discovery of the "muscoides-like" *Fucus* from sandy outer habitats in BBH, it was unknown from the Northwest Atlantic (cf. Sears 1998; South and Tittley 1986; Wynne and Magne 1991). The plant is a miniature alga that lacks a holdfast and forms an embedded turf or "moss-like carpets" (Norton and Mathieson 1983) in sandy sediments associated with *Spartina patens.* The ecology of *F. spiralis* in BBH is unique as it grows abundantly on outer sandy bluffs (i.e., psammophytically). By contrast, in nearby muddy estuaries (e.g., the Great Bay Estuary System), it only grows attached to scattered metamorphic and volcanic rock outcrops (Niemeck and Mathieson 1976). Attached populations of *F. vesiculosus* are restricted to scattered boulders and pilings (Table 1).

As noted above, three detached fucoid ecads are common in BBH, *Ascophyllum nodosum* ecad *scorpioides, Fucus vesiculosus* ecad *volubilis,* and *F. spiralis* ecad *lutarius.* The first two are the most abundant and widely distributed (Table 1), growing as entangled and/or embedded populations amongst culms of *Spartina alterniflora. Fucus spiralis* ecad *lutarius* occupies a similar habitat, but it is scattered and less abundant. Detached plants of *Fucus,* variously described taxonomically, have been reported since the 1880s from Long Island, New York, to Massachusetts (Taylor 1957). After comparing European materials, Chapman (1939) confirmed the presence of *F. spiralis* ecad *lutarius* from Scituate, Massachusetts, and *F. vesiculosus* ecad *volubilis* from Cold Spring Harbor, Long Island, New York, with the latter being based upon collections of Baker and Blandford in 1912. Chapman (1939) notes that few investigators record both detached Fucus ecads in New England salt marshes (cf. Webber and Wilce 1971). This generalization is particularly true for marshes north of Massachusetts; our investigations throughout Maine (Mathieson, Dawes, and Hehre, unpubl. data) indicate that both ecads are widely distributed within the state's salt marshes.

The introduced green alga *Codium fragile* subsp. *tomentosoides* is rare at nearshore coastal sites in New Hampshire and Maine (cf. Mathieson and Hehre 1986; Mathieson et al. 1993). However, it grows abundantly at several insular sites in the Gulf of Maine (e.g., the Isles of Shoals) but is previously unknown from estuarine habitats (Harris and Mathieson, in press). The occurrence of *Codium* in BBH ponds represents the first record of its abundant growth in a Maine salt marsh. The microscopic green alga *Urospora curvata* is newly recorded from nearshore coastal areas in Maine, being previously known from deep water habitats within the Gulf of Maine and southern Massachusetts (Grocki 1984; Sears and Cooper 1978). We found it growing epiphytically on *Ascophyllum nodosum* and *Fucus vesiculosus* at both Seapoint and BBH. The opportunistic brown alga *Melanosiphon intestinalis* is very prolific within BBH, particularly on slumping channel embankments. It is a seasonal annual that is most conspicuous during spring and early summer, being reduced in size and confined to small residual patches by mid-July. The plant also grows abundantly in many other Maine and New Hampshire tidal marshes (Mathieson, Dawes, and Hehre, unpubl. data), while it is uncommon at contiguous open coastal sites within the same two states. By contrast, *Melanosiphon* exhibits a broader coastal distribution in Massachusetts and southern New England (C. Schneider, pers. comm.).

In summary, the coastal and estuarine seaweed flora of southern Maine is highly diverse and exceeds or equals that of other northern New England regions, such as Penobscot Bay (Mathieson et al. 1996) and Mount Desert Island (Mathieson et al. 1998). Detached fucoid ecads and psammophytic populations of *Fucus spiralis* are common in BBH. New records for the "muscoides-like" *Fucus* and for *Urospora curvata* and *Codium fragile* subsp. *tomentosoides* are given.

ACKNOWLEDGMENTS. We acknowledge the help of several local residents who shared their knowledge about and provided access to the unique habitats of Brave Boat Harbor. Our thanks are also given to Franz Anderson and Larry Ward for their insights about BBH's geology. The present studies were supported in part by funds from the Leslie Hubbard Marine Endowment at the University of New Hampshire and the New Hampshire Agriculture Experiment Station. The paper is issued as Contribution Number 346 from the Jackson Estuarine Laboratory and the Center for Marine Biology. The first author acknowledges the encouragement and help of his wife, Myla Mathieson.

LITERATURE CITED

ADEY, W. H. AND P. J. ADEY. 1973. Studies of the biosystematics and ecology of the epilithic crustose Corallinaceae of the British Isles. Brit. Phycol. J. 8: 343–407.

ANONYMOUS. 1984. National Status and Trends Program for Marine Environmental Quality. NOAA, Washington, DC.

———. 1987. Strategic Assessment of Near Coastal Waters, Northeast Case Study. EPA/NOAA Team on Near Coastal Waters, Washington, DC.

———. 1996. Tide Tables 1996, High and Low Water Predictions, East Coast of North and South America, Including Greenland. U.S. Dept. Commerce, NOAA, Washington, DC.

APPOLONIO, S. 1979. The Gulf of Maine. Courier of Maine Books, Rockland, ME.

BAKER, S. M. AND M. H. BOHLING. 1916. On the brown seaweeds of the salt marsh. Part II. Their systematic relationships, morphology, and ecology. J. Linn. Soc. Bot. 43: 325–380.

BELKNAP, D. F., J. T. KELLEY, AND R. C. SHIPP. 1987. Quaternary stratigraphy of representative Maine estuaries: Initial examination by high-resolution seismic reflection profiling, pp. 177–207. *In*: D. N. Fitzgerald and P. S. Rosen, eds., Glaciated Coasts. Academic Press, San Diego, CA.

BIRD, C. J. AND J. L. MCLACHLAN. 1992. Seaweed Flora of the Maritimes 1. Rhodophyta—The Red Algae. Biopress Ltd., Bristol, England.

BLAIR, S. M. 1983. Taxonomic treatment of the *Chaetomorpha* and *Rhizoclonium* species (Cladophorales; Chlorophyta) in New England. Rhodora 85: 175–211.

BLIDING, C. 1963. A critical survey of European taxa in Ulvales, Part I. *Capsosiphon, Percursaria, Blidingia, Enteromorpha.* Opera Bot., Lund 8: 1–160.

———. 1968. A critical survey of European taxa in Ulvales, Part II. *Ulva, Ulvaria, Monostroma, Kornmannia.* Bot. Not. 121: 535–629.

BLOMSTER, J., C. A. MAGGS, AND M. J. STANHOPE. 1999. Extensive intraspecific morphological variation in *Enteromorpha muscoides* (Chlorophyta) revealed by molecular analysis. J. Phycol. 35: 575–586.

BOOTHROYD, J. C. 1978. Mesotidal inlets and estuaries, pp. 287–360. *In*: R. A. Davis, Jr., ed., Coastal Sedimentary Environments. Springer-Verlag, New York.

BRAY, J. R. AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325–349.

BURROWS, E. M. 1991. Seaweeds of the British Isles, Vol. 2. Chlorophyta. British Museum (Natural History), London.

CHAPMAN, V. J. 1939. Some algal complexities. Rhodora 41: 19–28.

COLEMAN, D. C. AND A. C. MATHIESON. 1975. Investigations of New England marine algae VII: Seasonal occurrence and reproduction of marine algae near Cape Cod, Massachusetts. Rhodora 77: 76–104.

COLLINS, F. S. 1894. Division II. Algae, pp. 227–249. *In*: E. L. Rand and J. H. Redfield, eds., A Preliminary Catalogue of the Plants Growing on Mount Desert Island and the Adjacent Islands. University Press, Cambridge, MA.

———. 1911. The marine algae of Casco Bay. Proc. Portland Soc. Nat. Hist. 2: 257–282.

COTTON, A. D. 1910. On the growth of *Ulva latissima* in water polluted by sewage. Bull. Misc. Inform. Kew, pp. 15–19.

COUTINHO, R. AND U. SEELIGER. 1984. The horizontal distribution of the benthic algal flora in the Patos Lagoon Estuary, Brazil, in relation to salinity, substratum and wave exposure. J. Exp. Mar. Biol. Ecol. 80: 247–257.

DIXON, P. S. AND L. M. IRVINE. 1977. Seaweeds of the British Isles, Vol. 1. Rhodophyta, Part 1: Introduction, Nemaliales, Gigartinales. British Museum (Natural History), London.

DOTY, M. S. 1948. The flora of Penikese, seventy-four years after. I. Penikese Island marine algae. Rhodora 50: 253–269.

——— AND J. NEWHOUSE. 1954. The distribution of marine algae into estuarine water. Amer. J. Bot. 41: 508–515.

DÜWEL, L. AND S. WEGEBERG. 1996. The typification and status of *Leptophytum* (Corallinaceae, Rhodophyta). Phycologia 35: 470–483.

FARLOW, W. G. 1881. Marine algae of New England. Rep. U.S. Comm. Fish and Fisheries for 1879, Washington, DC, Appendix A-1: 1–210.

FEMINO, R. J. AND A. C. MATHIESON. 1980. Investigations of New England marine algae IV. The ecology and seasonal succession of tide pool algae at Bald Head Cliff, York, Maine, USA. Bot. Mar. 23: 319–332.

FLETCHER, R. L. 1987. Seaweeds of the British Isles, Vol. 3, Part 1. Fucophyceae (Phaeophyceae). British Museum (Natural History), London.

FRALICK, R. A. AND A. C. MATHIESON. 1975. Physiological ecology of four *Polysiphonia* species (Rhodophyta, Ceramiales). Mar. Biol. 29: 29–36.

FRITSCH, F. E. 1935. The Structure and Reproduction of the Algae, Vol. I. Cambridge Univ. Press, Cambridge, England.

GROCKI, W. 1984. Algal investigations in the vicinity of Plymouth, Massachusetts, pp. 19–47. *In*: J. D. Davis and D. Merriman, eds., Observations on the Ecology and Biology of Western Cape Cod Bay, Massachusetts. Springer-Verlag, New York.

GRØEN, P. 1967. The Waters of the Sea. Van Nostrand Co. Ltd., Princeton, NJ.

GUO, Z. AND A. C. MATHIESON. 1992. Physiological ecology of four ulvoid green algae. Bot. Mar. 35: 523–533.

HARDWICK-WITMAN, M. 1985. Biological consequences of ice rafting in a New England salt marsh community. J. Exp. Mar. Biol. Ecol. 87: 283–298.

———. 1986. Aerial survey of a salt marsh: Ice-rafting to the lower intertidal zone. Estuarine Coastal Shelf Sci. 22: 379–383.

HARPER, J. T. AND G. W. SAUNDERS. 2000. A molecular systematic investigation of the taxonomic validity of the genus Euthora (Kallymeniaceae, Gigartinales), p. 21. *In*: Program and Abstracts 39th Northeast Algal Symposium, Northeast Algal Society, Dartmouth, MA.

HARRIS, L. G. AND A. C. MATHIESON. 1999. Patterns of range expansion, niche shift and predator acquisition in *Codium fragile* ssp. *tomentosoides* and *Membranipora membranacea* in the Gulf of Maine. Proc. Nat. Conf. Marine Bioinvasions (in press).

HARTOG, C. DEN. 1971. The border environment between the sea and the fresh water with special reference to the estuary. Vie & Milieu, Ser A, Biol. Mar. (Suppl.) 22: 739–751.

HEHRE, E. J., J. R. CONWAY, AND R. A. STONE. 1970. Flora of the Wolf Islands Part III: The marine algae. Rhodora 72: 115–118.

——— and A. C. Mathieson. 1970. Investigations of New England marine algae II. Composition, seasonal occurrence and reproductive periodicity of the marine Rhodophyceae in New Hampshire. Rhodora 72: 194–239.

Hoek, C. van den. 1963. Revision of the European Species of *Cladophora.* E. J. Brill, Leiden, Netherlands.

———. 1982. A Taxonomic Revision of the American Species of *Cladophora* (Chlorophyceae) in the North Atlantic Ocean and their Geographic Distribution. North Holland Publ. Co., Amsterdam.

Irvine, L. M. 1983. Seaweeds of the British Isles, Vol. 1. Rhodophyta, Part 2a. Cryptonemiales (*sensu stricto*), Palmariales, Rhodymeniales. British Museum (Natural History), London.

——— and Y. M. Chamberlain. 1994. Seaweeds of the British Isles, Vol. 1. Rhodophyta, Part 2b. Corallinales, Hildenbrandiales. British Museum (Natural History), London.

Jacobson, H. A. and G. L. Jacobson, Jr. 1989. Variability of vegetation in tidal marshes of Maine, U.S.A. Canad. J. Bot. 67: 230–238.

———, ———, and J. T. Kelley. 1987. Distribution and abundance of tidal marshes along the coast of Maine. Estuaries 10: 126–131.

Jerome, W. C. Jr., A. P. Chesmore, C. O. Anderson, Jr., and F. Grice. 1965. A Study of the Marine Resources of the Merrimack River Estuary. Monograph Ser. No. 1, Div. of Mar. Fish., Dept. of Natl. Res., Commonwealth of Massachusetts.

Jordan, D. S. 1874. The flora of Penikese Island. Amer. Naturalist 8: 193–197.

Josselyn, M. N. and J. A. West. 1985. The distribution and temporal dynamics of the estuarine macroalgal community of San Francisco Bay. Hydrobiologia 129: 139–152.

Kelley, J. T. 1987. An inventory of coastal environments and classification of Maine's glaciated shoreline, pp. 150–176. *In*: D. N. Fitzgerald and P. S. Rosen, eds., Glaciated Coasts. Academic Press, San Diego, CA.

Ketchum, B. H. 1983. Estuarine characteristics, pp. 1–14. *In*: B. H. Ketchum, ed., Ecosystems of the World, Vol. 26. Estuaries and Enclosed Seas. Elsevier Scientific Publ. Co., Amsterdam.

Kingsbury, J. M. 1969. The Seaweeds of Cape Cod and the Islands. Chatham Press Inc., Chatham, MA.

Kinne, O. 1970. Temperature, pp. 407–514. *In*: O. Kinne, ed., Marine Ecology, Vol. 1, Part 1. Wiley-Interscience, New York.

———. 1971. Salinity, pp. 821–995. *In*: O. Kinne, ed., Marine Ecology, Vol. 1, Part 2. Wiley-Interscience, New York.

Knight, M. and M. W. Parke. 1931. Manx algae: An algal survey of the south end of the Isle of Man. L. M. B. C. Memoirs 30: 1–155.

Lamb, I. M. and M. H. Zimmerman. 1964. Marine vegetation of Cape Ann, Massachusetts. Rhodora 66: 217–254.

Lewis, I. F. 1924. The flora of Penikese, fifty years after. Rhodora 26: 181–195.

Lewis, J. R. 1964. The Ecology of Rocky Shores. English Univ. Press, Ltd., London, England.

———. 1968. Water movements and their role in rocky shore ecology. Sarsia 34: 13–36.

LODER, T. C., J. E. HISLOP, J. P. KIM, AND G. M. SMITH. 1979. Hydrographic and Chemical Data for Rivers Flowing Into the Great Bay Estuary System, New Hampshire. Sea Grant Tech. Rep. UNH-SG-161, Sea Grant Program, Univ. New Hampshire, Durham, NH.

———, J. A. LOVE, J. P. KIM, AND C. G. WHEAT. 1983a. Nutrient and Hydrographic Data for the Great Bay Estuarine System, New Hampshire-Maine, Part II. January, 1976–June, 1978. Univ. New Hampshire Marine Program Publ., UNH-MP-D/TR-SG-83-4, Univ. New Hampshire, Durham, NH.

———, ———, C. E. PENNIMAN, AND C. D. NEEFUS. 1983b. Longterm Environmental Trends in Nutrient and Hydrographic Data From the Great Bay Estuarine System, New Hampshire-Maine. Univ. New Hampshire Marine Program Publ., UNH-MP-D/TR-SG-83-4, Univ. New Hampshire, Durham, NH.

MAGGS, C. A. AND M. H. HOMMERSAND. 1993. Seaweeds of the British Isles, Vol. 1. Rhodophyta, Part 3a. Ceramiales. British Museum (Natural History), London.

MANN, K. H. 1982. Ecology of Coastal Waters: A Systems Approach. Univ. California Press, Berkeley, CA.

MATHIESON, A. C. 1979. Vertical distribution and longevity of subtidal seaweeds in northern New England, U.S.A. Bot. Mar. 30: 511–520.

———. 1989. Phenological patterns of northern New England seaweeds. Bot. Mar. 32: 419–438.

———, C. J. DAWES, AND E. J. HEHRE. 1998. Floristic and zonation studies of seaweeds from Mount Desert Island, Maine: An historical comparison. Rhodora 100: 333–379.

——— AND R. A. FRALICK. 1972. Investigations of New England marine algae V. The algal vegetation of the Hampton-Seabrook Estuary and the open coast near Hampton, New Hampshire. Rhodora 74: 406–435.

——— AND ———. 1973. Benthic algae and vascular plants of the lower Merrimack River and adjacent shoreline. Rhodora 75: 52–64.

——— AND E. J. HEHRE. 1982. The composition, seasonal occurrence and reproductive periodicity of the marine Phaeophyceae in New Hampshire. Rhodora 84: 411–437.

——— AND ———. 1983. The composition and seasonal periodicity of the marine Chlorophyceae in New Hampshire. Rhodora 85: 275–299.

——— AND ———. 1986. A synopsis of New Hampshire seaweeds. Rhodora 88: 1–139.

———, ———, AND M. COSTA. 1993. Algal vegetation of the York River Estuary and the adjacent open coast of southern Maine. Rhodora 95: 285–324.

———, ———, J. HAMBROOK, AND J. GERWECK. 1996. A comparison of insular seaweed floras from Penobscot Bay, Maine, and other northwest Atlantic islands. Rhodora 98: 369–418.

———, ———, AND N. B. REYNOLDS. 1981. Investigations of New England marine algae I: A floristic and descriptive ecological study of the marine algae at Jaffrey Point, New Hampshire. Bot. Mar. 24: 521–532.

———, C. D. Neefus, and C. Emerich-Penniman. 1983. Benthic ecology in an estuarine tidal rapid. Bot. Mar. 26: 213–230.

——— and C. A. Penniman. 1986a. Species composition and seasonality of New England seaweeds along an open coastal-estuarine gradient. Bot. Mar. 29: 161–176.

——— and ———. 1986b. A phytogeographic interpretation of the marine flora from the Isles of Shoals, U.S.A. Bot. Mar. 29: 413–434.

——— and ———. 1991. Floristic patterns and numerical classification of New England estuarine and open coastal seaweed populations. Nova Hedwigia 52: 453–485.

———, ———, P. K. Busse, and E. Tveter-Gallagher. 1982. The effects of ice on *Ascophyllum nodosum* within the Great Bay Estuary System of New Hampshire-Maine. J. Phycol. 18: 331–336.

———, ———, and L. G. Harris. 1991. Northwest Atlantic rocky shore ecology, pp. 109–191. *In*: A. C. Mathieson and P. H. Nienhuis, eds., Ecosystems of the World, Vol. 24. Intertidal and Littoral Ecosystems. Elsevier Scientific Publ. Co., Amsterdam.

———, N. B. Reynolds, and E. J. Hehre. 1981. Investigations of New England marine algae II: The species composition, distribution and zonation of seaweeds in the Great Bay Estuary System and the adjacent open coast of New Hampshire. Bot. Mar. 24: 533–545.

———, E. Tveter, M. Daly, and J. Howard. 1977. Marine algal ecology in a New Hampshire tidal rapid. Bot. Mar. 20: 277–290.

Miller, B., D. Normandeau, G. Piehler, P. Hall, A. Mathieson, R. Fralick, D. Turgeon, P. Mahoney, and W. Owen. 1971. Ecological Study of Merrimack River Estuary—Massachusetts, Presented to the U.S. Army, Corps of Engineers by Normandeau Associates, Inc., Bedford, NH, and Viast Inc.

Niemeck, R. A. and A. C. Mathieson. 1976. An ecological study of *Fucus spiralis* L. J. Exp. Mar. Biol. Ecol. 24: 33–48.

Norall, T. L., A. C. Mathieson, and C. Emerich-Penniman. 1982. Nutrient and Hydrographic Data for the Great Bay Estuarine System, New Hampshire-Maine, Part I. September, 1973–December,1975. Jackson Estuarine Lab. Contrib. No. 150, UNH D/TR 178, Durham, NH.

Norton, T. A. and A. C. Mathieson. 1983. The biology of unattached seaweeds, pp. 333–386. *In*: F. E. Round and D. J. Chapman, eds., Progress in Phycological Research, Vol. 2. Elsevier Scientific Publ. Co., Amsterdam.

Penniman, C. A. and A. C. Mathieson. 1985. Photosynthesis of *Gracilaria tikvahiae* McLachlan (Gigartinales, Rhodophyta) from the Great Bay Estuary, New Hampshire. Bot. Mar. 28: 427–435.

Reynolds, N. B. and A. C. Mathieson. 1975. Seasonal occurrence and ecology of marine algae in a New Hampshire tidal rapid. Rhodora 77: 512–533.

Sawyer, C. M. 1965. The sea lettuce problem in Boston Harbor. J. Water Pollut. Control Fed. 37: 1122–1133.

Schneider, C. W. and R. B. Searles. 1991. Seaweeds of the Southeastern United States. Duke Univ. Press, Durham, NC.

Sears, J. R., ed. 1998. NEAS Keys to Benthic Marine Algae of the Northeastern Coast of North America from Long Island Sound to the Strait of Belle Isle. Contrib. 1, Northeast Algal Society, Dartmouth, MA.

——— AND R. A. COOPER. 1978. Descriptive ecology of offshore deep-water benthic algae in the temperate western North Atlantic Ocean. Mar. Biol. 44: 309–314.

——— AND R. T. WILCE. 1975. Sublittoral benthic marine algae of southern Cape Cod and adjacent islands: Seasonal periodicity, associations, diversity, and floristic composition. Ecol. Monogr. 45: 337–365.

SILVA, P. C., P. W. BASSON, AND R. L. MOE. 1996. Catalogue of the Benthic Marine Algae of the Indian Ocean, Vol. 79. Univ. California Press, Berkeley, CA.

SOUTH, G. R. 1983. Benthic marine algae, pp. 385–420. *In*: G. R. South, ed., Biogeography and Ecology of the Island of Newfoundland. Dr. W. Junk Publishers, The Hague, Netherlands.

——— AND R. G. HOOPER. 1980. A catalogue and atlas of the benthic marine algae of the island of Newfoundland. Mem. Univ. Nfld. Occas. Pap. Biol. 3: 1–136.

——— AND I. TITTLEY. 1986. A Checklist and Distributional Index of the Benthic Algae of the North Atlantic Ocean. Spec. Publ. Huntsman Mar. Lab. and British Museum (Natural History), St. Andrews, New Brunswick and London.

STEVENSON, J. C., L. G. WARD, AND M. S. KEARNEY. 1986. Vertical accretion in marshes with varying rates of sea level rise, pp. 242–259. *In*: D. A. Wolf, ed., Estuarine Variability. Academic Press, NY.

STONE, R. A., E. J. HEHRE, J. M. CONWAY, AND A. C. MATHIESON. 1970. A preliminary checklist of the marine algae of Campobello Island, New Brunswick, Canada. Rhodora 72: 313–338.

TAYLOR, W. R. 1957. The Marine Algae of the Northeastern Coast of North America. Univ. Michigan Press, Ann Arbor, MI.

TITTLEY, I., W. R. FARNHAM, G. R. SOUTH, AND D. KEATS. 1987. Seaweed communities of the Passamaquoddy region, southern Bay of Fundy, Canada. Brit. Phycol. J. 22: 313.

VILLALARD-BOHNSACK, M. 1995. Illustrated Key to the Seaweeds of New England. Rhode Island Nat. Hist. Surv., Kingston, RI.

WEBBER, E. E. AND R. T. WILCE. 1971. Benthic salt marsh algae at Ipswich, Massachusetts. Rhodora 73: 262–291.

WILKINSON, M. 1980. Estuarine benthic algae and their environments: A review, pp. 425–486. *In*: J. H. Price, D. E. G. Irvine, and W. F. Farnham, eds., The Shore Environment, Vol. 2. Ecosystems. Academic Press, NY.

WOELKERLING, W. J. 1973. The morphology and systematics of the *Audouinella complex* (Acrochaetiaceae, Rhodophyceae) in northeastern United States. Rhodora 75: 529–621.

WYNNE, M. J. AND J. N. HEINE. 1992. Collections of marine red algae from St. Matthew and St. Lawrence Islands, the Bering Sea. Nova Hedwigia 55: 55–97.

——— AND F. MAGNE. 1991. Concerning the name *Fucus muscoiodes* (Cotton) J. Feldmann *et* Magne. Cryptog. Algol. 12: 55–65.

APPENDIX

A SYNOPSIS OF STUDY SITES WITHIN SOUTHERN MAINE

OPEN COASTAL SITES (York and Kittery; Figure 2)

I. Cape Neddick (CN), Nubble Light. An exposed site with substrata consisting of massive outcrops and boulders grading into sand.

II. North bank of Brave Boat Harbor mouth (BBHN), York. An exposed open site with extensive boulders and relatively few rock outcrops and tide pools.

III. South bank of Brave Boat Harbor mouth (BBHS), Kittery. An exposed open site composed of coarse gravel and cobbles with few rock outcrops and tide pools. A highly dissected fringing marsh is also present.

IV. Seapoint (SP), Kittery. A semi-exposed spit of land on the seaward side of Cutts Island that experiences anthropogenic trampling year-round. The substrata are composed of rock outcrops, scattered boulder fields, sand, and cobbles; many tide pools are present at different elevations. The upper littoral zone slope changes with extensive seasonal sand deposition and erosion.

V. Sisters Point (SISP), Gerrish Island, Kittery. A semi-exposed site; substrata of boulders, cobbles, and scattered rock outcrops.

VI. Sewards Cove (SC), Gerrish Island, Kittery. A semi-exposed site; substrata the same as Sister's Point.

VII. Fort Foster (FF), Gerrish Island, Kittery. An outermost estuarine site (ca. 0.1 km inland) on the Piscataqua River, northeast of Wood Island. The substrata consist of scattered rock outcrops, boulders, cobbles, fragmented shale, and scattered fringing marshes.

BRAVE BOAT HARBOR (Figure 3)

Main Tidal Channel (i.e., between BBHN and BBHS). The northern side of the main channel is in York, while the southern side is in Kittery (km = distance inland from mouth).

1. York side of outer harbor (0.1 km). Cobbles and pebbles are present, plus a small, highly dissected fringing marsh.
2. York side of outer harbor (0.3 km). Situated near a sandy embayment (a flood tidal delta), downstream from old bridge pilings. Beds of blue mussels (*Mytilus edulis*) are present, as well as scattered small rocks and an expansive high salt marsh habitat. The latter shows extensive slumping.
3. Kittery side of outer harbor on Cutts Island (0.37 km) behind a coastal berm that forms a sandy embayment (a flood tidal delta). There are high and fringing marshes, scattered bedrock, and an extensive boulder field with a sharp slope (ca. 70°). At low tide, fresh water runoff from the high marsh flows into the central channel and out to the sandy embayment.
4. Kittery side of outer harbor (0.38 km). Upstream from a set of old

bridge pilings and near the mouth (W side) of tributary #1, which delineates Cutts Island.

5. Kittery side of outer harbor on Cutts Island (0.39 km). Next to a set of old bridge pilings and near the mouth of tributary #1. The pilings provide an excellent substratum for seaweeds and are located in an area of tidal currents. Deep pools support a variety of seaweed taxa. Extensive slumping and erosion of the marsh is evident.
6. York side of outer harbor (0.40 km). There is a fringing marsh, located within a sandy embayment (a flood tidal delta) on the backside of a coastal berm.
7. York side of outer harbor near old bridge pilings (0.42 km).
8. Kittery side of outer harbor (0.48 km). The site is located on Cutts Island behind a coastal berm within a sandy embayment (a flood tidal delta).
9. Kittery side of harbor (0.65 km). The high marsh has slumped and exposed the remains of old wooden pilings and tree stumps, providing habitats for various seaweeds. The tidal slopes and channels are muddy with a little sand.
10. York side of harbor near the mouth of a small embayment (0.67 km).
11. York side of harbor near the mouth of a small tributary (0.85 km).
12. Kittery side of harbor just upstream from the mouth of a small tributary (0.86 km).
13. Kittery side of harbor just downstream from the mouth of tributary #3 (1.07 km). A high marsh and tidal mudflat are present.
14. York side of harbor just downstream from the old bridge pilings at Beddell Crossing (1.11 km). The channel below the bridge is initially narrow, then expands to form a flat bed that contains small boulders, cobbles, and gravel, as well as mud, detritus, and limited amounts of sand. Algae grow on the gentle slopes and in the channel on rocks. This is close to the headwaters of the harbor, and fresh water flows out during low tide, resulting in very low salinities (less than 10 ppt). In the winter, the area is usually frozen.
15. York side of harbor just downstream from tributary #3 and within an embayment area (1.23 km).
16. Kittery side near the old bridge pilings at Beddell Crossing (1.3 km); a small tidal rapids flows from a high tide pool.
17. York side of harbor near the old Beddell Crossing bridge pilings (1.4 km).
18. Kittery side of harbor near the culvert at Brave Boat Harbor Road (1.57 km).
19. York side of harbor near the culvert on Brave Boat Harbor Road (1.6 km); a concrete embankment and boulders are present.
20. York side of inner harbor (1.8 km), on Payne Road just west of Brave Boat Harbor Road.
21. York side of inner harbor just beyond the culvert on Brave Boat Harbor Road (1.9 km).

Tributary #1: The main tributary on the Kittery side of Brave Boat Harbor that delineates Cutts Island. Distances are from the mouth of Brave Boat Harbor and Sewards Cove, respectively.

1a. Upstream from site #10 at an embayment on the north side of the tributary (0.53 and 4.2 km).
1b. Upstream from site #10 on Cutts Island (S side) near the first major junction (0.91 and 3.8 km); a narrow tidal channel and significant currents.
1c. Upstream from the first major junction on the north side (0.96 and 3.7 km); a large circular channel is present merging into high pools.
1d. The second major junction on the south side (1.46 and 3.5 km); a tidal channel with strong currents and contiguous salt marsh.
1e. An inner riverine site on the north side with a narrow channel near a branch of the second major junction (1.46 and 3.23 km).
1f. A narrow channel on the north side with a tributary at the end of the second major junction near Brave Boat Harbor Road (1.52 and 3.17 km).
1g. The third major junction (1.55 and 3.14 km); a tidal channel with strong currents falling in both directions (see text), plus contiguous salt marshes.
1h. The end of a small meandering channel near Brave Boat Harbor Road (1.75 and 2.94 km); a contiguous high marsh is present.
1i. Approximately 0.17 km from Seapoint Road (1.83 and 2.9 km); a narrow channel with strong tidal currents, plus adjacent high marsh.
1j. The bridge culvert on Seapoint Road; strong tidal currents, excellent rocky substratum and a fringing marsh are present (2.0 and 2.27 km).

Tributary #2: The second major tributary, and the only one located on the York side of Brave Boat Harbor. Distances (km) are from the mouth of the Harbor.

2a. Approximately 0.23 km upstream from site #15 off the main Harbor channel (1.5 km); a tidal channel with a contiguous high salt marsh.
2b. Approximately 0.47 km upstream from site #15 off the main Harbor channel (1.74 km); an upper tidal channel with fresh water discharge.

Tributary #3: The third major tributary, and the second one located on the Kittery side of Brave Boat Harbor. Distances (km) are from the mouth of the Harbor.

3a. Approximately 0.06 km upstream from the mouth of tributary #3 on the west side (1.26 km).
3b. Directly across from #3a (1.3 km) on the east side.
3c. Approximately 0.23 km upstream from the mouth of tributary #3 on the west side at the first major junction (1.5 km).
3d. The west side of tributary #3 near Brave Boat Harbor Road (1.82 km); an upper tidal channel with fresh water drainage.

Tributary #4: Chauncey Creek and contiguous salt marshes separating Gerrish and Cutts Island, Kittery. Distances (km) from Sewards Cove.

4a. At the junction of Seapoint Road and the bridge crossing Chauncey Creek to Gerrish Island (2.4 km); a shady, narrow channel, with scattered boulders.

4b. Approximately 0.15 km east of Seapoint Road bridge, near an old retaining wall or dam (2.48 km); strong tidal currents and contiguous mudflats and fringing marshes.

4c. A transition from a broad tidal mudflat to a narrow channel; this is a mudflat with scattered pebbles and a contiguous salt marsh (3.2 km).

4d. Near an oxbow and a major tidal junction (3.5 km); a narrow vertical channel with contiguous high marshes is present here.

4e. At the end of the northernmost tidal channel east of site #4d (4.0 km); a narrow vertical channel with contiguous high marshes.

4f. At the end of the southernmost tidal channel east of site #4d (3.9 km); a vertical tidal channel with a contiguous upper salt marsh.

4g. A inner salt marsh located behind a conspicuous coastal berm near Seapoint Beach, just east of site #4e (4.21 km).